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DISTRIBUTION, ABUNDANCE, AND AGE AND GROWTH OF THE TOMTATE, *HAEMULON AUROLINEATUM*, ALONG THE SOUTHEASTERN UNITED STATES COAST[1]

CHARLES S. MANOOCH III[2] AND CHARLES A. BARANS[3]

ABSTRACT

Tomtates, *Haemulon aurolineatum*, were widely distributed over sponge-coral habitats throughout the South Atlantic Bight region in depths of 9 to 55 m, although they were occasionally caught in large numbers over sandy bottom habitats. Fish were most common in offshore areas during winter and were not taken in waters of <10°C south of Cape Fear, N.C. Juveniles (≤148 mm TL) were caught in the same geographical areas as adults, but were collected in warmer waters than adults during fall and winter. Spawning occurred during the spring.

Individuals collected by hook and line and trawl were aged by scales and otoliths. Back-calculated mean total lengths were from 103.0 mm at age I, to 280.5 at age IX. The von Bertalanffy growth equation is $l_t = 310\,(1 - \exp - 0.22017\,(t + 1.28))$, where t is age in years, and l_t is total length at age. The oldest fish sampled was age IX, 289 mm TL. Annual total mortality based on catch curves from 1,496 fish landed by the recreational fishery from 1972 to 1978 was 59% (instantaneous total annual mortality = 0.89). We found that the tomtate grows faster, does not live as long, and has a higher natural mortality rate than most other reef fishes previously studied in the South Atlantic Bight.

The tomtate, *Haemulon aurolineatum*, is a small grunt (Haemulidae), which occurs from Cape Cod, Mass., to Brazil, including the Caribbean, Gulf of Mexico, and Central American coast. The species, previously referred to as *Bathystoma rimator*, *B. aurolineatum*, and *Haemulon rimator* (Courtenay 1961), is known vernacularly as xira in Brazil; cuji in Venezuela; rancho, juez, and chankay in Mexico; and mulita, mula, mariquita, and maruca in Puerto Rico.

The tomtate is taken primarily by hook and line off the southeastern United States and by traps, hook and line, and trawl in the more southern areas of its range. Unfortunately, commercial landings of tomtates in the United States are reported in the collective term "grunts," which includes many different species of the family and therefore precludes species identifications that are needed for fishery management. A Soviet-Cuban cooperative fisheries research program on the Campeche Banks revealed the tomtate as the main demersal species caught by trawl from 1962 to 1972 (Sokolova 1969; Sauskan and Olaechea 1974). Also, exploratory trawling off South Carolina found large quantities of tomtates (Wenner et al. 1979a).

Recreational headboat[4] fishermen fishing from North Carolina to Cape Canaveral, Fla., caught an average of 23.2 t (metric tons) of tomtates in 1976 and 1977 (Dixon[5]). This species was the most commonly caught haemuline, although second in weight landed to the white grunt, *Haemulon plumieri*.

In this paper we describe the relative abundance, spatial and temporal distributions, spawning, age, growth, and mortality for tomtates along the southeastern United States.

METHODS

Distribution and Relative Abundance

Eight groundfish survey cruises spanning all four seasons (Table 1) were conducted on the con-

[1]Contribution No. 192, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA; No. 189, MARMAP Program; No. 127, South Carolina Marine Resources Center, Marine Resources Institute.

[2]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[3]South Carolina Wildlife and Marine Resources Department, Marine Resources Research Institute, Charleston, SC 29412.

[4]A boat for hire where anglers are charged on a per person basis.

[5]R. L. Dixon, Southeast Fisheries Center Beaufort Laboratory, NMFS, NOAA, Beaufort, NC 28516, pers. commun. January 1978.

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TABLE 1.—Groundfish cruises of the RV *Dolphin*.

Cruise	Dates	No. of trawls	No. of tows with tomtates	No. of tomtates
DP-7305	23 Oct.-16 Nov. 1973	86	18	2,075
DP-7402	1 Apr. - 9 May 1974	112	19	442
DP-7403	13 Aug.-19 Sept. 1974	87	14	581
DP-7501	16 Jan. -10 Apr. 1975	92	10	1,212
DP-7503	30 Aug.-19 Sept. 1975	87	20	1,298
DP-7601	12 Jan. - 7 Feb. 1976	86	15	4,005
DP-7603	28 Aug.-21 Sept. 1976	89	15	1,749
DP-7701	17 Jan. - 9 Mar. 1977	93	11	3,260

tinental shelf and upper continental slope between Cape Fear, N.C., and Cape Canaveral, Fla., except in spring 1974 when sampling extended to Cape Hatteras. A preassigned number of stations was selected randomly (Grosslein 1969) with a set number in each of six depth zones (9-18 m; 19-27 m; 28-55 m; 56-110 m; 111-183 m; 184-366 m). Bottom water temperatures were measured at each station with mechanical or expendable bathythermographs.

Thirty-minute trawls were made continuously (day and night) from the RV *Dolphin*, at 6.5 km/h with a towing wire scope of 2.5-3.0:1. The trawl was a 3/4-scale version of a "Yankee No. 36" with a 16.5 m footrope, 11.9 m headrope, and 1.3 cm stretch mesh cod end liner (Wilk and Silverman 1976).

Fork lengths (later converted to total lengths) of all fish collected by trawl were recorded to the nearest centimeter. Frozen fish samples were taken to the laboratory for further investigations.

An index of relative abundance (Musick and McEachran 1972) was calculated for each depth zone by the following expression:

$$\text{Index of Relative Abundance} = \frac{\Sigma \ln (x+1)}{n_h}$$

where n_h = number of trawls in the hth depth zone, and x = number of individuals for each tow in a given depth zone. Because previous investigators have shown that trawl catches are usually distributed as a negative binomial (Elliott 1971; Taylor 1953), a $\ln (x+1)$ transformation was made on the relative abundance data to permit statistical tests to determine if the differences among habitats within depth zones were significant.

Estimates of biomass standing stock were calculated with both transformed, $\ln (x+1)$, and untransformed data for comparison of the resulting values. The stratified mean catch/tow (Cochran 1977) was calculated by the expression:

$$\bar{y}_{st} = \frac{1}{N} \sum_{h=1}^{k} [N_h \bar{y}_h]$$

where $\bar{y}_{st}$ = stratified mean catch(kg)/tow,
N = total area,
N_h = area of hth depth zone (from planimeter chart measurements),
$\bar{y}_h$ = mean catch/tow in the hth depth zone, and
k = number of zones in the set.

The area of live-bottom habitat in each depth zone (≈14.5%) was estimated from the frequency of occurrence of sponge and coral in catches during 5 yr of bottom trawling with the stratified random sampling design. The areas of sandy-bottom habitats were obtained by subtraction. The estimated population variance of the mean catch(kg)/tow was also calculated by Clark and Brown (1977):

$$S^2 = \frac{1}{N} \sum_{h=1}^{k} [N_h \bar{y}_h^{\,2}] - N\bar{y}_{st}^{\,2} + \sum_{h=1}^{k} S_h^{\,2} \left[(N_h - 1) + \frac{(N_h - N)}{N} \frac{(N_h - n_h)}{n_h} \right]$$

where S^2 = estimated population variance, and
$S_h^{\,2}$ = variance of the hth zone.

The mean catch/tow ($\bar{y}_h$) of the transformed $\ln (x+1)$ data was estimated for each depth zone following the methodology of Bliss (1967):

$$E(\bar{y}_h) = \exp (\bar{y}_h + S_h^2/2)$$

where $E(\bar{y}_h)$ = the estimated (retransformed) mean catch(kg)/tow in the hth depth zone, $\bar{y}_h$ and S_h^2, both expressed in logarithmic units, are the zone mean and its variance. The same methodology was applied to obtain the stratified mean catch/tow from transformed data for the whole study area. Biomass estimates were expanded by the area swept method (Rohr and Gutherz 1977), using

$$SS_{tot} = \sum_{h=1}^{k} (\bar{P}_h)\ (A_h)$$

where SS_{tot} = total standing stock,

$\bar{P}_h$ = average population expressed as kilograms per km^2 in the hth depth zone, and

A_h = total area of the hth depth zone.

The sweep of the "3/4 Yankee trawl" was 8.748 m (Azarovitz[6]), and 3.241 km was the distance covered during a standard trawl. It should be noted that all estimates were minimum estimates because the sampling efficiency of our gear with regard to tomtates was unknown. Standing stock values calculated for sandy-bottom areas incorporated such a large number of zero catches that the transformation did not normalize the data, so the resulting values should be considered suspect.

Age and Growth

Scales, otoliths, fish lengths, and fish weights were collected from 1,496 tomtates from the recreational headboat fishery operating from North Carolina to Cape Canaveral from 1972 through 1978 and from approximately 100 juvenile fish collected by research trawling off South Carolina. Total fish length was recorded in millimeters and weight in grams.

Scales were removed from beneath the tip of the posteriorly extended pectoral fin, soaked in a one-tenth aqueous solution of phenol, cleaned and mounted dry between two glass slides, and viewed at 40× magnification on a scale projector. Measurements were made and recorded from the scale focus to each annulus and to the scale edge in the anterior field for marginal increment analyses and back-calculating fish length at the time of annulus formation.

Otoliths (sagittae) were removed by making a transverse cut in the cranium with a hacksaw midway between the posterior edge of the orbit and the preopercle. The skull was pried open and the otoliths were removed with forceps, washed in water, and stored dry in labeled vials. Rings were counted by placing the otoliths in a blackened-bottom watch glass and then viewing the structures through a binocular dissecting microscope with the aid of reflected light. Some of the otoliths from large (older) fish were sectioned with a Buehler, Isomet, 11-1180[7] low-speed saw to facilitate aging. Measurements were not recorded from otoliths since these structures were used only as a method of validating age determined by reading scales.

Lengths by age for fish from all years combined were back-calculated from a scale radius-fish length regression. The regression equation was based on the relationship of magnified (40×) scale length to total fish length. Since a majority of the scale measurements were clustered around a relatively narrow size range, we based our regression on a subsample of scale radius and body length measurements. After grouping the measurements into 25 mm body length intervals, we selected approximately 12 from each interval to ensure that the regression provided good representation. The prediction equation took the form $TL = a\ SR^b$; where TL = total length, SR = scale radius, a = intercept, and b = slope. We substituted the means of the distances from the focus to each annulus for SR in the above equation, calculated the mean fish length for the time of each annulus formation, and then calculated mean growth increment for each age group.

Calculation of a theoretical growth curve is useful in modeling of growth in natural populations of fish. Growth parameters such as theoretical maximum attainable size (L_∞), growth coefficient (K), and theoretical time of the beginning of growth (t_0), may be used in constructing population models. The most popular theoretical growth curve, the von Bertalanffy ($l_t = L_\infty(1 - \exp -K(t - t_0))$) was fitted to back-calculated length at age data (Ricker 1975; Everhart et al. 1975). This particular equation also allows us to make comparisons with results obtained by other researchers.

The growth parameter, L_∞, was first derived by fitting a Walford (1946) line: $l_{t+1} = L_\infty(1 - k) + kl_t$ to back-calculated data where l_t = total length at age t, and k = slope of the Walford line. The slope (k) is equal to e^{-k}, thus our first estimate of $K = \ln k$. Preliminary values of L_∞ were obtained by solving the equation $L_\infty = y$-intercept / $(1 - k)$, and by regressing annual growth increment (X) against fish length at the beginning of the incremental period (Y) (Jones 1976). By plotting $\log_e(L_\infty - l_t)$ against t and by using trial values of L_∞ ranging from lower than the prelimi-

[6]T. Azarovitz, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, Mass., pers. commun. January 1978.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

nary values to much greater, we determined the best L_∞ that resulted in the straightest line. The growth coefficient (K) was the slope of this line and was used to solve for t_0:

$$t_0 = \frac{\text{y - intercept of natural log line - } \log_e L_\infty}{K}.$$

We checked the t_0 value to see if it was biased toward younger or older fish by using the equation $t_0 = t(1/K) \ln (1 - l_t/L_\infty)$ for separate ages I-IX (Jones 1976).

Mortality Estimates

We calculated annual total mortality estimates by analyzing catch curves (Beverton and Holt 1957) based on fully recruited age fish and older. If the $\log_e$ of the age frequency in the catch is plotted on age, the slope of the linear descending right limb of the curve is equal to the mean instantaneous total mortality (Z). To calculate mortality rates, we first needed to assign ages to the 1,100 or so unaged fish. We grouped fish of known age by 25 mm length intervals, calculated the percentage of fish of each observed age in each group, and used these percentages to estimate the number of fish of each age for the unaged group (Ricker 1975).

Length-Weight and Fork Length-Total Length Relationships

To calculate length-weight and length conversion relationships fish lengths were subsampled to provide a fairly equal distribution throughout the size range of fish examined during this study. The length-weight relationship was expressed exponentially, whereas the fork length-total length equation was expressed as a simple linear regression.

Spawning

Gonads were examined macroscopically by season to determine the approximate time of spawning. Observations on the development of testes were used collaboratively with measurements recorded from ovaries. Ovaries were weighed to calculate a seasonal gonad index, or the percentage of gonad weight to fish weight.

RESULTS

Distribution and Relative Abundance

Tomtates were collected throughout the South Atlantic Bight (Figs. 1-4). Although most of the continental shelf is sandy "open-shelf habitat" (Struhsaker 1969), the greatest catches of tomtates were directly associated with the irregularly distributed sponge-coral ("live bottom") habitats (as defined by Wenner et al. 1979a). Indices of relative abundance over live-bottom areas were significantly larger ($P<0.01$) than abundance indices from sandy-bottom catches in all seasons and years, except during the cold winter of 1977 (Table 2). Although tomtates occurred in 30-70% of the collections from the sponge-coral habitat, 79.6% of the total number caught during seven cruises, excluding the cold winter of 1977, were at sponge-coral stations (Table 3).

During all seasons, catches of tomtates over sand were infrequent, but occasionally large (Wenner et al. 1979a, b, c, d). Occurrence of tomtates in both sandy-bottom and live-bottom habitats increased the difficulty in biomass estimations. Information from catches over the sponge-coral habitat with the 30-min tows was expanded to preliminary estimates of biomass (Tables 4, 5), although the catch represented a mixed habitat collection of unknown proportions. Standing crop estimates of tomtates from the region between Cape Fear and Cape Canaveral ranged from 1,730 t (minimum catch, summer 1974) to 12,878 t (maximum catch, winter 1976). Although biomass estimates were calculated separately for each depth zone and standing crop estimates were calculated separately for catches from live-bottom and sandy-bottom habitats (Table 6), all estimates represent minimal values because fish availability and vulnerability to the trawl were not considered.

Tomtates, both juvenile (<137 mm TL) and adult, were more abundant in catches in the northern part of the South Atlantic Bight than in catches in the south. During all seasons sampled, between 1973 and 1977, the catch north of lat. 32°32′N, an arbitrary shelf division, was between 59 and 89% of the total catch. The one exception occurred during the cold winter of 1977, when 98% of the total catch (3,192 fish) was made south of lat. 32°30′N at a single station.

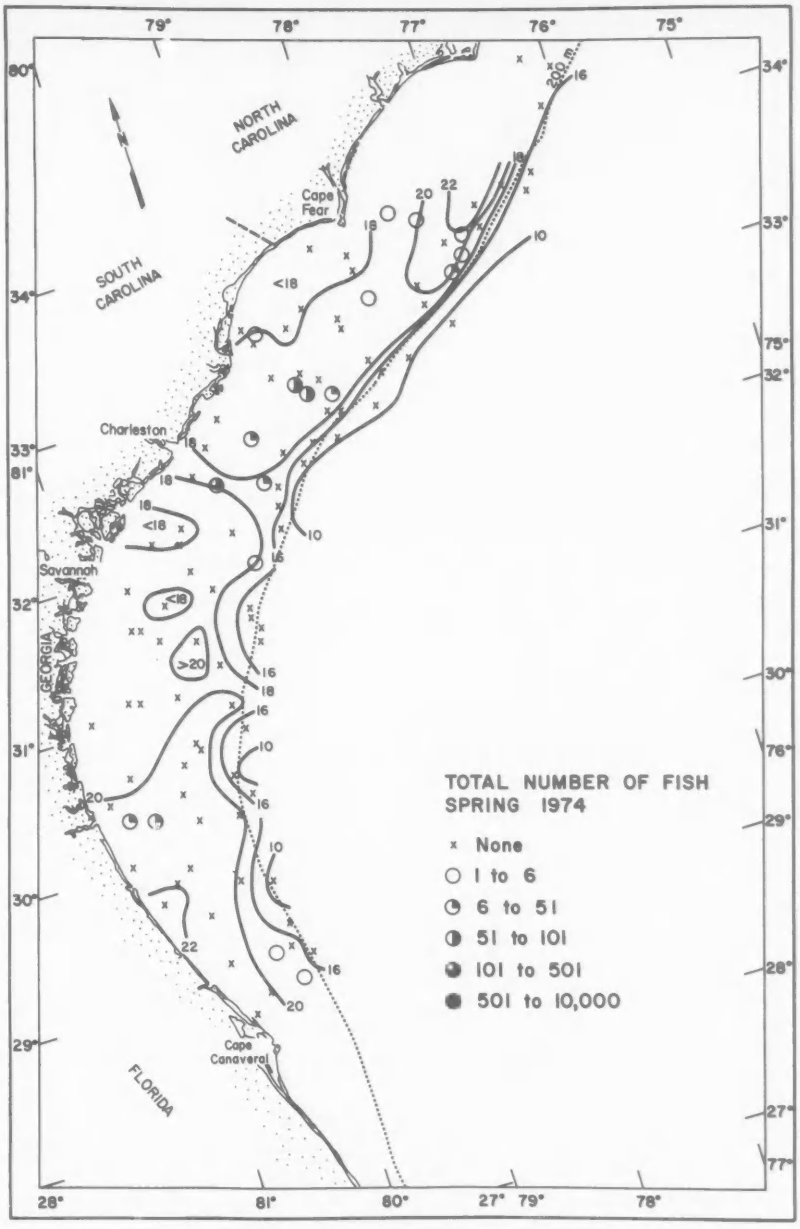

FIGURE 1.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral, 1 April-9 May 1974.

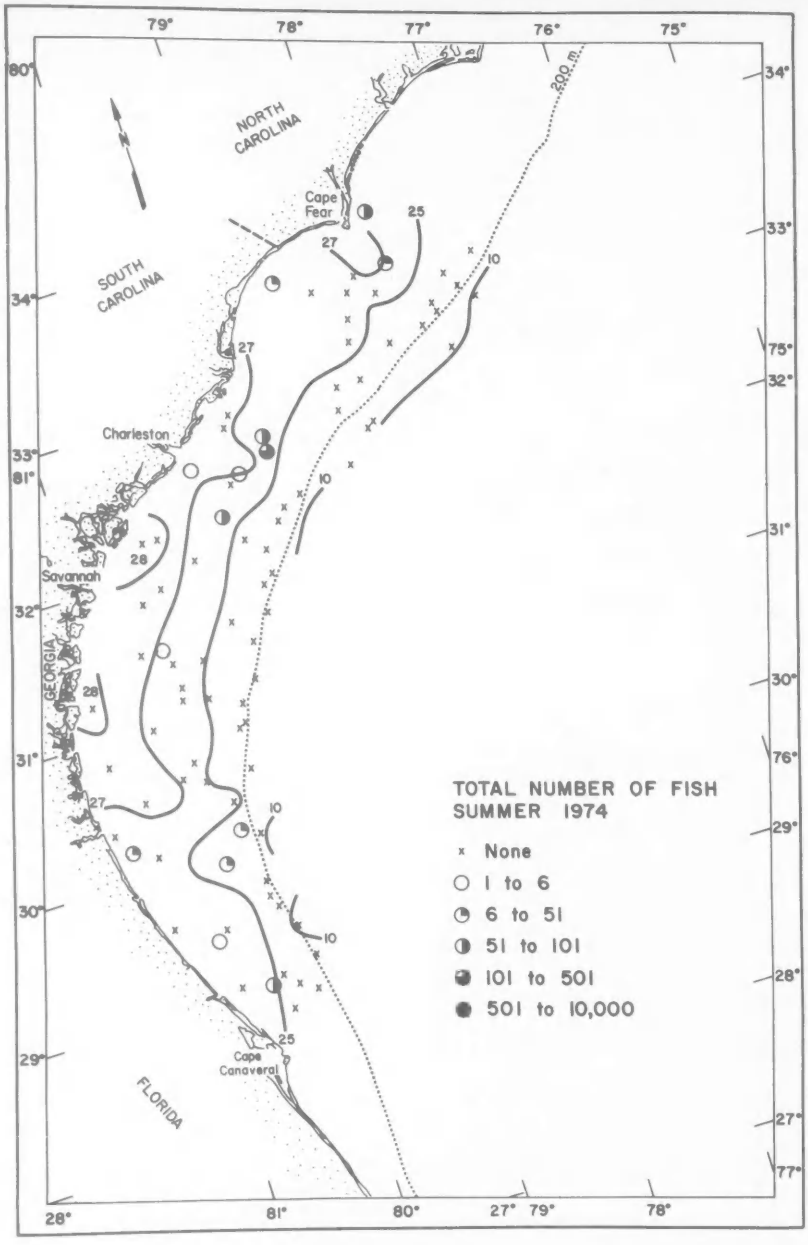

FIGURE 2.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral, 13 August-19 September 1974.

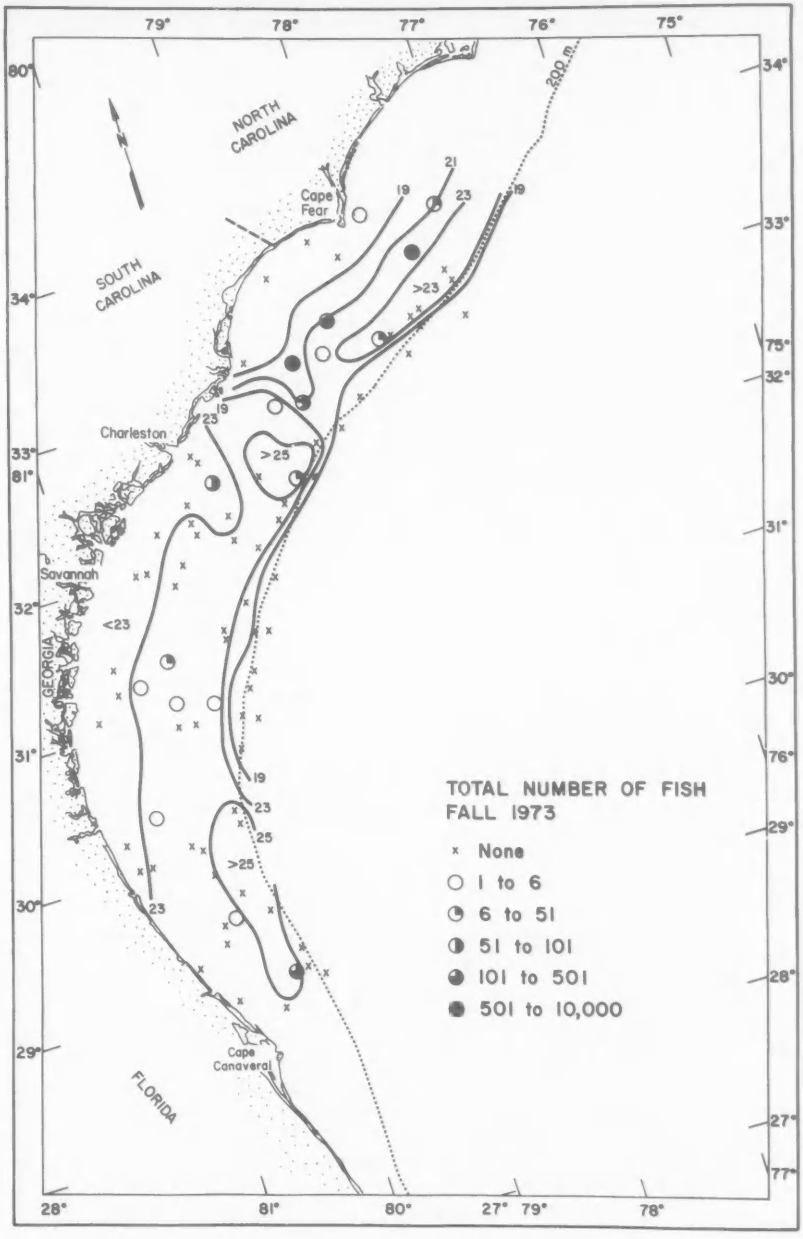

FIGURE 3.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral, 23 October-16 November 1973.

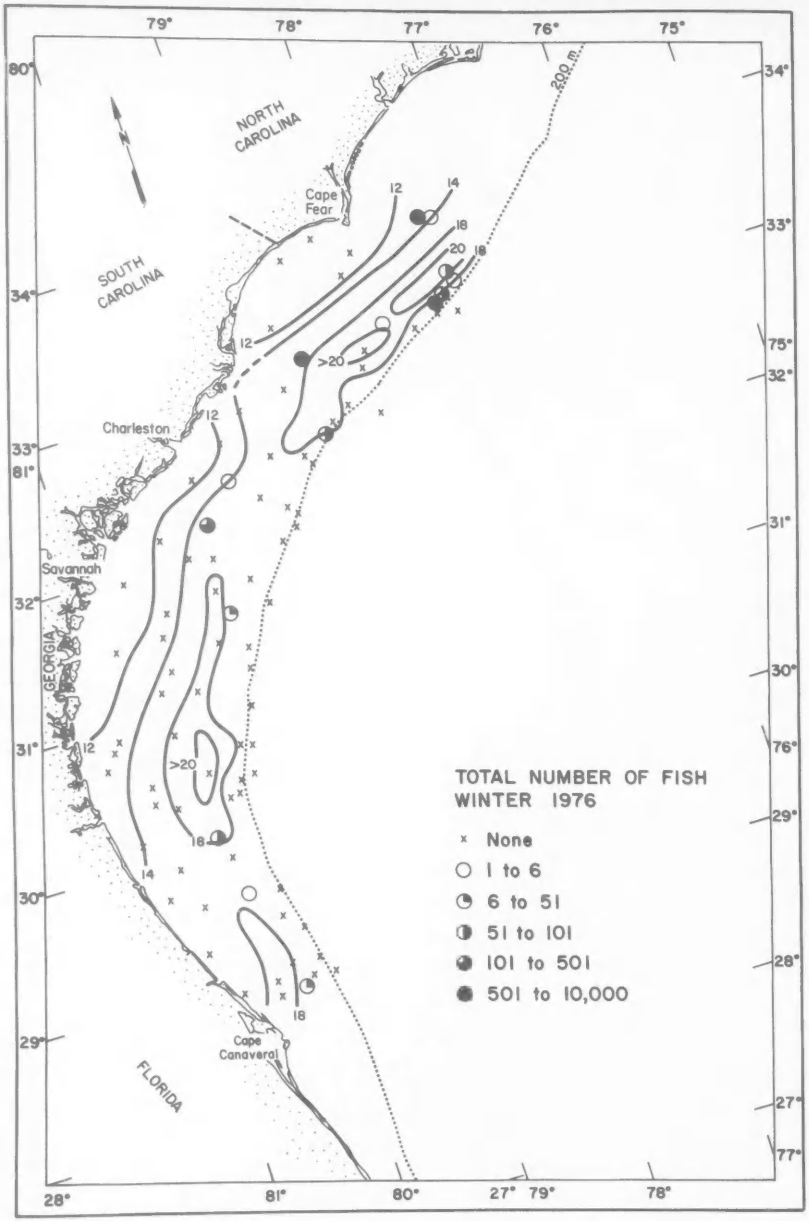

FIGURE 4.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral, 12 January-7 February 1976.

TABLE 2.—*t*-test and chi-square results of comparisons between numbers of tomtates in catches over live-bottom and sandy-bottom habitats.

Seasons	*t*-test of $\frac{\Sigma \ln(x+1)}{n}$	df	χ^2 test of $\frac{\Sigma x}{n}$	df
Fall 1973	3.75**	65	14.79**	1
Spring 1974	4.70**	55	15.69**	1
Summer 1974	4.15**	66	24.73**	1
Winter 1975	2.83**	68	93.36**	1
Summer 1975	8.18**	66	69.46**	1
Winter 1976	8.77**	67	350.41**	1
Summer 1976	11.04**	67	193.32**	1
Winter 1977	1.59n.s.	70	40.42**	1

** = significant at 0.01 level; n.s. = nonsignificant at 0.05 level.

TABLE 3.—Catches of tomtates associated with collections within the "live bottom"-sponge/coral habitats.

Cruise date	Live bottom stations: *N*	Live bottom stations: % with tomtates	Tomtate catch: Total number	Tomtate catch: % from live bottom
Fall 1973	10	39	2,075	29.6
Spring 1974	11	42	442	55.7
Summer 1974	14	50	581	76.2
Winter 1975[1]	9	30	1,212	78.4
Summer 1975	18	70	1,298	98.2
Winter 1976	11	53	4,005	97.6
Summer 1976	8	53	1,749	91.7
Winter 1977[2]	11	55	3,260	1.5
Average		50		79.6

[1]Sampling season prolonged into spring.
[2]Unusually cold winter, data omitted from average.

TABLE 4.—Mean catch/tow ($\bar{y}_s$) values for trawl-caught tomtates on untransformed and transformed [ln (kg + 1)] data by depth and habitat zone for summer 1974. Bliss' (1967) estimation of the mean was applied to the transformed values.

Depth (m)	Habitat	$\bar{y}_s$ biomass (kg/tow) untransformed	$\bar{y}_s$ biomass (kg/tow) transformed	Area of zone (km^2)	No. of tows
9-18	live	5.272	12.981	2,622	2
	sand	0.324	0.163	15,461	14
19-27	live	6.804	6.804	2,730	1
	sand	0.218	0.101	16,100	18
28-55	live	3.991	5.196	3,794	5
	sand	0.000	0.000	22,367	14
56-110	live	1.285	1.120	692	6
	sand	0.000	0.000	4,083	8

TABLE 5.—Mean catch/tow ($\bar{y}_s$) values for trawl-caught tomtates on untransformed and transformed [ln (kg + 1)] data by depth and habitat zone for winter 1976. Bliss' (1967) estimation of the mean was applied to the transformed values.

Depth (m)	Habitat	$\bar{y}_s$ biomass (kg/tow) untransformed	$\bar{y}_s$ biomass (kg/tow) transformed	Area of zone (km^2)	No. of tows
9-18	live	0.000	0.000	2,622	2
	sand	0.000	0.000	15,461	15
19-27	live	104.848	110.616	2,730	3
	sand	0.000*	0.000*	16,100	13
28-55	live	5.450	5.465	3,794	2
	sand	0.133	0.130	22,367	19
56-110	live	2.675	3.163	692	4
	sand	0.001	0.001	4,083	11

TABLE 6.—Minimum standing crop estimates of tomtates in the South Atlantic Bight during summer 1974 and winter 1976. All values should be expanded by 10^2; units are in metric tons. LCL and UCL = lower and upper 90% confidence limits, respectively.

	Untransformed			Transformed		
	Mean($\bar{Y}$st)	LCL	UCL	Mean($\bar{Y}$st)	LCL	UCL
Summer 1974						
sand bottom	3.00	0.02	5.98	2.53	1.05	4.19
live bottom	17.08	7.14	27.02	21.39	8.46	48.36
total area	20.08			23.92		
Winter 1976						
sand bottom	1.05	0.23	1.87	1.02	0.39	1.70
live bottom	108.86	13.39	204.34	127.76	46.71	342.13
total area	109.91			128.78		

Tomtates were collected at depths ranging from 13 to 91 m. The greatest relative abundance of both juveniles and adults in the South Atlantic Bight was consistently within the three shallowest (<55 m) depth zones (Fig. 5). The depth distributions of juveniles and adults indicated a slight shift offshore during winter but did not indicate major seasonal movements of fish within the South Atlantic Bight region. During winters (1975-77), tomtates were not collected in the nearshore (9-18 m) zone. In summer 1976, only adults were caught in the deep 56-110 m depth zone. During fall 1973 and winter 1977, only juveniles were collected in the 56-110 m depth zone, while in winter 1976, juveniles were much more abundant than adults in this depth zone.

Tomtates were collected at bottom temperatures from 10.3° to 28.1°C, but were seldom caught at temperatures <13°C. Differences in thermal distributions of juvenile (≤148 mm TL) and adult tomtates in the South Atlantic Bight indicated separate thermal preferences. During fall (1973) and winter (1976), the proportion of juveniles to adults in the total catch increased at

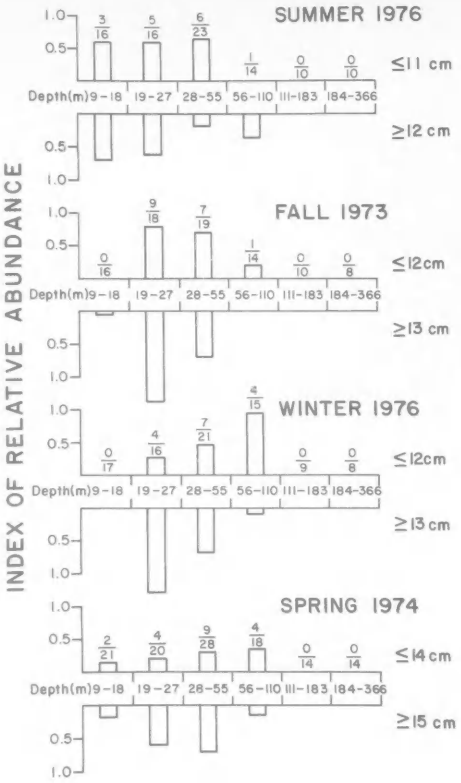

FIGURE 5.—Index of relative abundance for tomtates by depth zone during four seasons (juveniles above the axis, adults below: fraction numerator = number of trawls with tomtates; denominator = total number of trawls in depth zone).

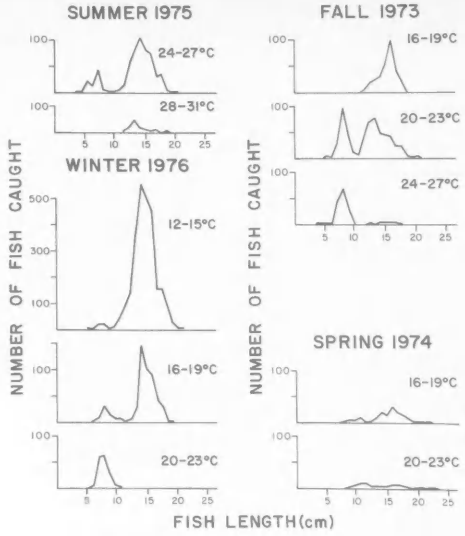

FIGURE 6.—Length-frequency distributions (TL) of tomtates by bottom water temperature interval (4°C).

higher temperature intervals (Fig. 6). Young tomtates (20-63 mm) have previously been collected during December in the Florida Keys at a water temperature of 16.2°C (Springer and Woodburn 1960). During summer (1975), juveniles were collected only in the coolest thermal zone (24.0°-27.9°C), while during spring (1974), both juveniles and adults were collected in the same thermal interval (16.0°-23.9°C).

Tomtates may avoid water temperatures of <10°C. Fish were never caught at <10.3°C during any season, even at five sponge-coral stations in areas where large numbers were caught at >10°C during the previous winter (Fig. 7).

Age and Growth

Validity of Rings as Annuli

Both scales and otoliths were used to age tomtates. Approximately 75% (397 of 529) of the scale samples and 85% (177 of 208) of the otoliths were legible. Since tomtates have been aged by reading scales (Sokolova 1969), we did not try specifically to validate the methods presented here. Several findings, however, pursuant to the goals of this paper, indicate that rings on tomtate scales and otoliths are true annuli. Close examination of otoliths from young-of-year tomtates, collected by trawl, clearly show the formation of one ring per year, and that the first ring (annulus) forms between the fall and spring collection periods.

The mean length of fish progressively increased as the number of scale or otolith rings increased and otoliths and scales agreed closely (Table 7). For instance, if aged by scales, age-I fish averaged 135.4 mm TL; age-II, 181.9; age-III, 203.3; age-IV, 220.0; age-V, 234.5; age-VI, 255.7; and age-VII, 265.8. If aged by otoliths, age-I fish averaged 134.3 mm TL; age-II, 164.7;

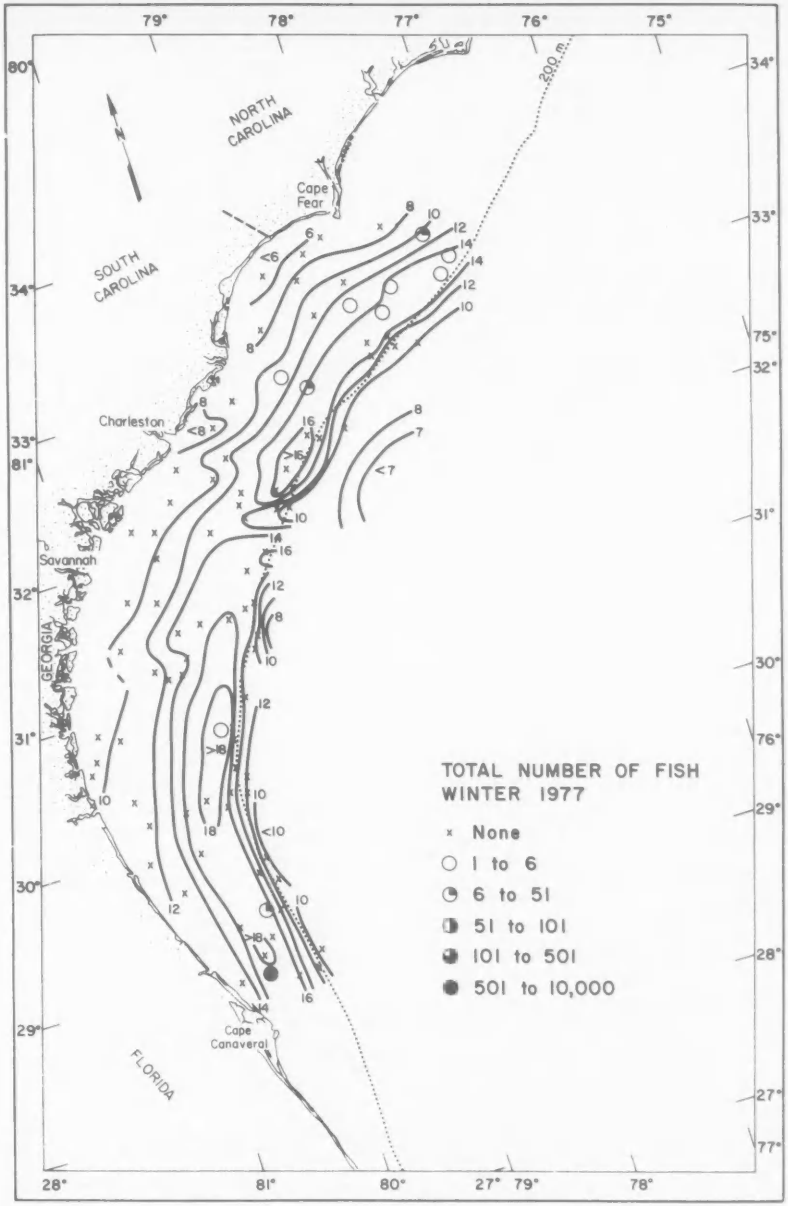

FIGURE 7.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral during the cold winter of 1977.

TABLE 7.—Comparison of mean empirical length-age data obtained by reading tomtate scales and otoliths.

	Scales				Otoliths				
Age group	N	Mean TL (mm)	Range in length (mm)	SD	N	Mean TL (mm)	Range in length (mm)	SD	Difference in means (mm)
0	22	84.7	50-142	28.1	54	89.8	50-142	29.9	5.1
1	9	135.4	109-171	25.6	23	134.3	80-157	21.5	1.1
2	45	181.9	153-206	13.3	43	164.7	150-185	9.7	17.2
3	81	203.0	180-221	9.6	16	197.1	161-212	14.7	5.9
4	134	220.0	195-238	10.5	19	213.0	193-227	11.1	7.0
5	66	234.5	208-257	11.3	12	232.2	226-242	4.1	2.3
6	28	255.7	245-268	6.3	9	253.1	240-262	6.5	2.6
7	5	265.8	260-272	5.5	1	267.0	—	—	1.2
8	4	277.0	270-280	5.0					
9	3	286.7	282-289	4.0					
Total	397								

age-III, 197.1; age-IV, 213.0; age-V, 232.2; age-VI, 253.1; and age-VII, 267.0 mm.

The relative length frequencies of the measured distance from the focus of the scale to each ring progressively increased with the number of rings. Significant features of the plotted curves were the occurrence of one mode for each ring, the consistent location of a specific mode on the X-axis for fish of different ages, the increased overlap for each additional ring, and the progressive decrease in the distance between modes for each successive year, indicating less linear growth each year as the fish ages.

Growth

There was relatively little difference in the mean annual increments of fish aged by scales and those of fish aged by otoliths (Table 7). Annual growth increments for fish aged by scales for ages I-V were: I-II, 46.5 mm; II-III, 21.1 mm; III-IV, 17.0 mm; and IV-V, 14.5 mm. After age V, growth appears to be more irregular, probably a result of the relatively small sample sizes for ages VI, VII, VIII, and IX (Table 7).

Lengths by age for fish from all years were back-calculated from a scale radius-fish length regression. The prediction equation was

$$TL = 1.7489\ SR^{0.9572};\ r = 0.93 \text{ and } N = 103,$$

where TL = total length, and SR = scale radius. By substituting the means of the distances from the focus to each annulus for SR in the above equation, we were able to calculate the mean fish length at the time of each annulus formation, and the mean annual growth increment for each age (Table 8).

The von Bertalanffy equation was used to describe theoretical growth. The growth parameters L_∞ and K were first calculated by fitting a Walford (1946) line to back-calculated data. The equation was $l_{t+1} = 90.833 + 0.6747_{l_t}$, $r = 0.982$. Our first estimate of K was l_n 0.6747 or 0.3935. This value was used to obtain L_∞ by solving the equation $L_\infty = y\text{-intercept} / (1 - k)$. The initial value for L_∞ of 289, and the subsequent value of 285.7 obtained by regressing annual growth increment (X) against fish length at the beginning of the incremental period (Y) (Jones 1976),

TABLE 8.—Calculated total lengths (millimeters) of 346 tomtates aged by scales.

Observed age	N	Mean calculated total length at end of year								
		1	2	3	4	5	6	7	8	9
I	9	103.7								
II	45	108.1	173.0							
III	75	102.5	171.1	199.1						
IV	123	102.6	168.4	198.8	214.1					
V	56	101.0	167.8	200.7	216.7	226.7				
VI	26	102.2	165.5	198.8	221.1	235.7	245.1			
VII	5	99.6	165.3	200.9	224.4	240.8	251.3	258.8		
VIII	4	105.3	171.7	195.5	215.1	228.6	242.0	252.1	260.8	
IX	3	102.5	170.6	200.9	222.1	237.7	253.0	264.5	273.5	280.5
Total	346									
Weighted mean		103.0	169.3	199.3	216.0	230.4	246.2	258.0	266.2	280.5
Increment		103.0	66.3	30.0	16.7	14.4	15.8	11.8	8.2	14.3
No. calculations		346	337	292	217	94	38	12	7	3

seemed low. Therefore, we plotted $\log_e (L_\infty - l_t)$ against t by using trial values of L_∞ ranging from 285 to 310 mm. The straightest line resulted from L_∞ of 310 mm. The slope of the line, −0.22017, was selected as the growth coefficient (K) and was used to obtain t_0 (−1.28). Our best estimate of the equation describing the theoretical growth of tomtates is

$$l_t = 310\ (1 - \exp - 0.22017(t + 1.28)).$$

Observed, back-calculated, and theoretical lengths at age are presented in Table 9.

TABLE 9.—Total lengths of tomtates at age (observed, back-calculated, and theoretical).

	Length at age (mm)		
Age	Observed	Back-calculated	Theoretical
1	135.4	103.0	122.4
2	181.9	169.3	159.4
3	203.0	199.3	189.2
4	220.0	216.0	213.1
5	234.5	230.4	232.2
6	255.7	246.2	247.6
7	265.8	258.0	259.9
8	277.0	266.2	269.8
9	286.7	280.5	277.8

Mortality Estimates

By age IV, tomtates are fully recruited to the hook and line fishery, the only important method of harvesting this species off the southeastern United States. Instantaneous mortality (Z) estimates were obtained by analyzing catch curves of fish aged IV and older (Fig. 8). The mean total annual mortality estimate for 1972 through 1978 was 59% ($Z = 0.887$). By year, instantaneous mortality rates were 1974, 0.669; 1975, 1.035; 1976, 1.017; 1977, 1.041; and 1978, 0.972. Too few fish were sampled from the fishery in 1972 and 1973 to construct catch curves. The instantaneous mortality rate(s) for tomtates was higher than those previously obtained for white grunt, $Z = 0.65$ (Manooch 1976), or for red porgy, $Z = 0.58$ (Manooch and Huntsman 1977).

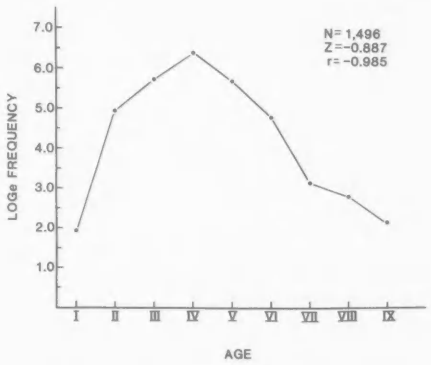

FIGURE 8.—Catch curve for tomtates caught by hooked line off the southeastern United States, 1974-77.

Length-Weight and Fork Length-Total Length Relationships

Fish ranging from 52 to 280 mm TL were used to calculate a length-weight relationship. The equation

$$W = 0.0000086L^{3.0905},\ r = 0.996 \text{ and } N = 70,$$

where W = weight in grams and L = total length in millimeters, describes this relationship. The equation $TL = -1.8196 + 1.1540\ FL$, $r = 0.99$ and $N = 100$ was derived to convert lengths.

Spawning

Indirect evidence indicates that tomtates of the South Atlantic Bight spawn primarily in April and May. Running ripe males and partly spent females were caught in April 1979 (28-42 m; 16.4°-19.4°C), while a major decrease in mean ovarian weight and maximum ovary weight of mature females occurred after the spring (April 1974) sampling period (Table 10). Throughout the year, many (>38%) of the females sampled each season were in the maturing and ripe condition. The presence of juveniles (33-90 mm TL; mode 80 mm) in bottom trawl collections during summer, and the progressive increase in modal fish lengths in length-frequency distributions

TABLE 10.—Gonad condition of adult tomtates (>15 cm TL) from the South Atlantic Bight.

Season	Sex	N	Running ripe %	Mean ovarian wt. (g)	Gonad index[1]	Maximum ovarian wt. (g)
Summer 1974	F	31	5	0.6	0.6	1.7
Fall 1973	F	45	2	0.5	0.5	1.4
Winter 1976	F	36	9	1.3	1.1	8.6
Spring 1979[2]	M	13	77	—	—	—
	F	34	0	4.2	3.4	17.0

[1]Gonad index = (ovary wt./fish wt.) × 100.
[2]Females 77% with hydrated eggs.

through a seasonal cycle (Fig. 9), indicated that these juveniles were spawned in spring.

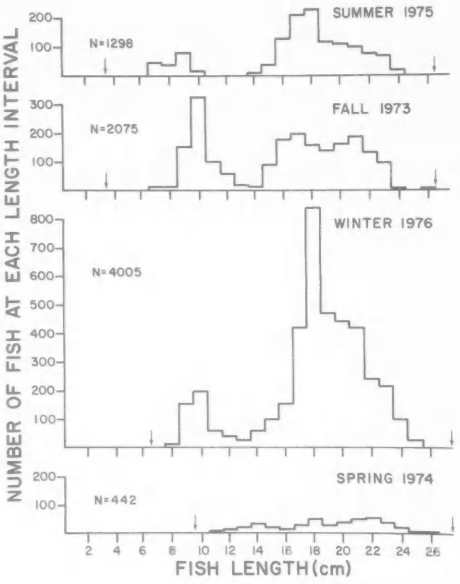

FIGURE 9.—Length-frequency distributions (FL) from the total catch of tomtates between Cape Fear and Cape Canaveral during each of four seasons.

DISCUSSION

Distribution and Abundance

Tomtates are considered abundant in several habitats in and to the south of the South Atlantic Bight, and indicate daily movements between habitats. Within the Bight, tomtates were common over both live-bottom and shelf-edge habitats during earlier (1959-64) exploratory fishing (Struhsaker 1969). Farther south, tomtates were found over broad sandy areas off southern Florida (Craig 1976), near coral stacks in the Tortugas Islands (Longley and Hildebrand 1941), and in grass beds and other open areas in the Bahamas (Bohlke and Chaplin 1968). Tomtates were common from nearshore to the offshore reefs in Florida and were abundant on the shrimp grounds of the Dry Tortugas and the Gulf of Mexico (Courtenay 1961). In the Virgin Islands, changes in distribution with respect to habitat type were associated with feeding behavior. Tomtates feed as individuals or in small schools at night over open sand (Collette and Talbot 1972), and they spend the day on the reef segregated into size groups; juveniles school over the highest part of the reef, while adults hover low between the coral colonies (Smith and Tyler 1972).

Juvenile tomtates may occur in several habitats, either inshore or offshore, which include "live bottom" and rocky outcrops similar to those occupied by adults. Small tomtates (≈33 mm) were abundant over artificial reefs (Parker et al. 1979) and natural ridges in spring through fall off the Carolinas and have been found in the mouths and stomachs of black sea bass in the same areas (Parker[8]). Young tomtates also frequent grass beds (Randall 1968), subtidal mud flats (Reid 1954), and nearshore areas around wharfs (Jordan and Evermann 1896). The presence of young fish among spines of sea urchins (Johnson 1978) suggests that microhabitats may be important to the survival of some early life stages. Juveniles of French grunts, *H. flavolineatum*, and white grunts, *H. plumieri*, form large multispecies schools closely associated with particular coral formations (microhabitats) during the day and follow precise routes (≥100 m) to and from feeding areas (sea grass beds) at night (Ogden and Ehrlich 1977).

Biomass and standing stock calculations for tomtate from groundfish trawling were considered preliminary, minimal estimates. More satisfactory estimates should incorporate information on 1) abundance/biomass sampling conducted completely within a known area of a given habitat type, 2) the correct proportional allocation of a day/night catch factor for each habitat sampled, 3) the vulnerability of tomtate to the sampling gear, and 4) estimates of biomass from untrawlable, rocky outcrop, habitats. Unfortunately, none of the above information is available at present, so our estimates were based upon continuous day/night sampling imposed on the very random nature of sponge-coral habitat distribution. Discrete, short duration trawling completely within the boundaries of the patchy sponge-coral habitats could be directed by pretrawl bottom mapping with underwater TV

[8]R. O. Parker, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516, pers. commun. January 1978.

(Powles and Barans 1980). This method would allow more accurate quantification of relative abundance differences between habitats and between day and night sampling. Then, a biomass factor could be developed to proportion fish availability to the trawl during daytime collections in sponge-coral habitats and during night in sand bottom habitats. Also, the vulnerability of tomtate, or any groundfish in the South Atlantic Bight, to trawl gear is unknown. Several experiments with a headrope mounted TV system would do much to fill this data gap. Biomass estimates from rocky habitats may have to be extrapolated from nearshore diver counts or offshore TV counts, but many problems remain in the interpretation of these data. In general, a composite estimate of tomtate biomass or standing stock in the South Atlantic Bight should include difficult to obtain fish behavior information.

Tomtate are relatively shallow water (<50 m) groundfish with a more pronounced tendency for annual depth migrations in populations south of the South Atlantic Bight. Tomtates in the Campeche Bank area were most abundant in waters <30 m during all seasons (Sauskan and Olaechea 1974), while tomtates occurred only at depths of <10 m in the Bahamas (Bohlke and Chaplin 1968). Although tomtates remain inshore during winter in Florida (Courtenay 1961), they are not caught by inshore shrimp trawlers off South Carolina (Keiser 1976) and appear to avoid shallow waters (<20 m) north of Florida during winter. There is the possibility that during extremely cold winters, slight migrations (shifts in distribution) southward occur.

In contrast to the results of this study, tomtates of the Campeche Bank move onshore during winter and fall and offshore in spring and summer and are recruited to the fishery in shallow waters, a great distance from the deeper area where spawning takes place (Sauskan and Olaechea 1974). The difference in location of spawning and recruitment and lack of large adult fish over reefs in Florida (Stone et al. 1979) and in commercial trawl catches (Sokolova 1969) suggests separation of juvenile and adult populations, especially south of Florida.

Age and Growth

The fact that scales may be used to accurately determine the age of a warmwater marine fish species is not particularly surprising. Scales have been used to age other reef fishes that occur with tomtates in the South Atlantic Bight. Manooch (1976) found annuli on scales from white grunt collected off the Carolinas; Manooch and Huntsman (1977) aged red porgy, *Pagrus pagrus*, using both scales and otoliths; and Grimes (1978) determined the age of vermilion snapper, *Rhomboplites aurorubens*, by reading scales.

The theoretical parameters derived in this study are compared with those for tomtates from the Campeche Banks, and with cooccurring species in the South Atlantic Bight in Table 11. The Campeche Banks fish did not live as long—5 or 7 yr compared with 9 in the South Atlantic Bight—and had a slightly smaller maximum size (L_∞), 295 mm compared with 310 mm. Consequently, the growth coefficient, although very similar, is slightly higher—0.235 compared with 0.200. With the exception of black sea bass, *Centropristis striata*, sympatric species previously studied in the South Atlantic Bight were longer lived and slower growing (Table 11).

TABLE 11.—Growth parameters for six species of demersal fish.

Common name	Scientific name	Area	Author	M	K	L_∞ (TL, mm)	Longevity (yr)
Tomtate	*Haemulon aurolineatum*	N.C., S.C., Ga., east coast Florida	This paper		0.22017	310	9
		Campeche Banks	Calculated from Sokolova (1969)		0.235	295	5
			Sauskan and Olaechea (1974)				7
White grunt	*H. plumieri*	N.C., S.C.	Manooch (1976)	0.4 & 0.6	0.108	640	13
Red porgy	*Pagrus pagrus*	N.C., S.C.	Manooch and Huntsman (1977)	0.2	0.096	763	15
Vermilion snapper	*Rhomboplites aurorubens*	N.C., S.C.	Grimes (1976)	0.25	0.198	627	10
Gag	*Mycteroperca microlepis*	N.C., S.C., Ga., east coast Florida	Manooch and Haimovici (1978)	0.20	0.121	1,290	13
Black sea bass	*Centropristis striata*	N.C., S.C.	Mercer[1]	0.30	0.220	352	8

[1]Linda Mercer, Virginia Institute of Marine Sciences, Gloucester Point, Va.

Spawning

Growth rates of juvenile tomtates (≥130 mm TL/first year) in the South Atlantic Bight and rates estimated from larvae of similar species support the spawning season indicated by analysis of gonads. If growth of very early stages of tomtates approximates the 14 mm SL/30 d for white grunts (Saksena and Richards 1975) and French grunts (Brothers and McFarland In press), tomtates of 30-90 mm TL caught in early September may have been spawned between early April and June. Identification of peak spawning period of tomtate by associated larval abundance was impossible due to difficulties in identifying larval haemulids.

Populations of tomtates farther south appear to have a prolonged spawning season. Munro et al. (1973) reported collections of ripe females between January and August in Jamaica, while Cervigon (1966) suggested that tomtates spawn throughout the year in Brazil. Tomtates from Campeche Bank spawn primarily during July-September at depths of >50 m and again during winter at shallower depths (Sauskan and Olaechea 1974).

Management

We believe management of the tomtate fishery should be considered for three reasons. First, the species is easily captured by a variety of fishing techniques: hook and line, trap, and unlike most other reef fishes, by trawl. Second, fishing effort applied to this, and other associated, species will probably increase. And third, the tomtate is a member of a rather delicate faunal community and is a major source of food for higher trophic level, piscivorous fishes. Unwise harvest of one species could have both physical and energetic impacts on the community as a whole.

While regional catches of tomtates may at times be quite large, for instance by recreational anglers on headboats fishing inshore waters, the species ranks low in terms of poundage landed in the South Atlantic Bight by both recreational and commercial fishermen. Because tomtates are small and not competitive in value with other reef fishes in the commercial market, commercial hook and line fishermen usually discard the species or use it as bait for larger predatory fishes, such as groupers and snappers (Wenner[9]).

Given the geographical range of *H. aurolineatum*, its abundance as indicated by exploratory trawling, and relatively low harvest by fishermen, one could label it as an "underutilized species" in the South Atlantic Bight. However, assigning tomtates this status requires a thorough understanding of currently operating fisheries plus a knowledge about the role of the species in the ecosystem. We do not recommend such a designation at this time.

Although the distribution of tomtate is continuous from the southeastern coast of the United States to the Campeche Banks, the stock fished in each area should be considered separate for assessment and fishery management. Our study and the studies of Sokolova (1969) and Sauskan and Olaechea (1974) show that tomtates are a relatively short-lived, fast-growing reef fish with a high annual mortality rate when compared with other reef fishes of the region. Fish with these biological traits usually are not as readily overfished as those that grow more slowly, those that live longer, and those with a lower annual mortality rate. However, many fast-growing, high-mortality species such as mackerels (*Scomberomorus*), some tunas (*Thunnus*), and menhaden (*Brevoortia*), which are important to large fisheries, have demonstrated some signs of being overfished.

By comparing our study with those on the Campeche Bank, we can look at one stock caught at present primarily by hook and line and the other by a more intensive gear, the trawl. The major difference between the South Atlantic Bight tomtates and those from Campeche Bank is that the Atlantic stock is older and larger. There are several explanations other than biological changes in ecology or genetics for the differences between these stocks. In our study, the tomtates were caught by recreational fishermen using hook and line while those from Campeche Bank were trawled. Hook and line fishing may be more selective of larger fish and some of the smaller fish may be discarded by the fishermen resulting in larger fish of each age being sampled. A more likely explanation is that the large, old Atlantic fish have a generally low exploitation rate. The Soviet-Cuban trawlers have fished Campeche Bank since 1964 with catches of grunts averaging over 20,000 tons a year and ex-

[9]C. A. Wenner, South Carolina Wildlife and Marine Resources Department, Marine Resources Research Institute, Charleston, SC 29412, pers. commun. January 1978.

ceeding 60,000 in 1971 and 1975 for the region according to FAO Yearbooks. If, as we suspect, most of these catches were tomtate, the Campeche stock has been much more exploited than the Atlantic for the past 10 yr.

Regional harvest of tomtates by hook and line will probably remain low. Recreational anglers will continue to catch small numbers, and commercial handliners will continue to regard *H. aurolineatum* as "trash fish" or bait. Any increase in the harvest will probably involve an expansion of a trawl fishery off South Carolina, Georgia, and northeast Florida.

Prior to development of any U.S. groundfish trawl fishery for tomtate, the possibility of habitat destruction by trawl gear should be investigated. Some bottom trawl harvest techniques may have detrimental effects on the substrate community in which tomtate are most abundant. Destruction or removal of the sponge/coral invertebrates and crab species, or damage to *Oculina* coral beds, may indirectly reduce future yields of tomtate and other fish species.

Also, during several seasons trawls may catch juveniles of a species important to both commercial and sport fisheries prior to their recruitment to harvest by hook and line. Bottom trawling for tomtate in "live bottom" areas would catch large numbers of small, commercially unimportant fish species and invertebrates which would increase costs of sorting unless the entire catch was processed as a mixed species product.

In our study the greatest relative abundance (catch/tow) of adults was during winter at which time commercial harvesting could take advantage of any concentrations of fish resulting from a shift to a more offshore distribution of the population. Reduction of fishing effort during late winter and early spring would allow the unfished stock to spawn and juveniles to be recruited to the fishery at a larger size, possibly regulated by net mesh size. Even in this case, a drastic reduction in population size could adversely affect the recreational headboat fishery.

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LITERATURE CITED

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.) Ser. II, 19, 533 p.

BLISS, C. I.
1967. Statistics in biology. Statistical methods for research in the natural sciences. Vol. 1. McGraw-Hill, N.Y., 558 p.

BOHLKE, J. E., AND C. C. G. CHAPLIN.
1968. Fishes of the Bahamas and adjacent tropical waters. Livingston Publ. Co., Wynnewood, Pa., 771 p.

BROTHERS, E. B., AND W. N. MCFARLAND.
In press. Correlations between otolith microstructure, growth, and life history transition in newly recruited French grunts [*Haemulon flavolineatum* (Demarest), Haemulidae]. Rapp. P.-V. Réun. Cons. Int. Explor. Mer.

CERVIGON M., F.
1966. Los peces marinos de Venezuela, Vol. II. Fundacion La Salle de Ciencias Naturales, Caracas, p. 449-951.

CLARK, S. H., AND B. E. BROWN.
1977. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963-74, as determined from research vessel survey data. Fish. Bull., U.S. 75:1-21.

COCHRAN, W. G.
1977. Sampling techniques. 3d ed. Wiley, N.Y., 428 p.

COLLETTE, B. B., AND F. H. TALBOT.
1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: Ecology of coral reef fishes, p. 98-124. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 14.

COURTENAY, W. R., JR.
1961. Western Atlantic fishes of the genus *Haemulon* (Pomadasyidae): Systematic status and juvenile pigmentation. Bull. Mar. Sci. Gulf Caribb. 11:66-149.

CRAIG, A. K.
1976. Trapping experiments with snappers in South Florida. *In* H. R. Bullis, Jr. and A. C. Jones (editors), Proceedings: Colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean, p. 222-236. Fla. Sea Grant Rep. 17, 333 p.

ELLIOT, J. M.
1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. 25, 144 p.

EVERHART, W. H., A. W. EIPPER, AND W. D. YOUNGS.
1975. Principles of fishery science. Cornell Univ. Press, Ithaca, N.Y., 288 p.

GRIMES, C. B.
1976. Certain aspects of the life history of the vermilion

snapper, *Rhomboplites aurorubens* (Cuvier), from North and South Carolina waters. Ph.D. Thesis, Univ. North Carolina, Chapel Hill, 240 p.

1978. Age, growth, and length-weight relationship of vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina waters. Trans. Am. Fish. Soc. 107:454-456.

GROSSLEIN, M. D.

1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.

JOHNSON, G. D.

1978. Development of fishes of the mid-Atlantic Bight: An atlas of egg, larval and juvenile stages, vol. IV. Carangidae through Ephippidae. U.S. Fish Wildl. Serv., Biol. Serv. Program FWS OBS-78/12, 314 p.

JONES, R.

1976. Growth of fishes. *In* D. H. Cushing and J. J. Walsh (editors), The ecology of the seas, p. 251-279. W. B. Saunders Co., Phila.

JORDAN, D. S., AND B. W. EVERMANN.

1896. The fishes of North and middle America: A descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. U.S. Natl. Mus. Bull. 47:1-3313.

KEISER, R. K., JR.

1976. Species composition, magnitude and utilization of the incidental catch of the South Carolina shrimp fishery. S.C. Mar. Resour. Cent. Tech. Rep. 16, 94 p.

LONGLEY, W. H., AND S. F. HILDEBRAND.

1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on color, habits, and local distribution. Carnegie Inst. Wash. Publ. 535, Pap. Tortugas Lab. 34, 331 p.

MANOOCH, C. S., III.

1976. Age, growth and mortality of the white grunt, *Haemulon plumieri* Lacépède (Pisces: Pomadasyidae), from North Carolina and South Carolina. Proc. Annu. Conf. Southeast. Assoc. Game Fish. Comm. 30:58-70.

MANOOCH, C. S., III, AND M. HAIMOVICI.

1978. Age and growth of the gag, *Mycteroperca microlepsis*, and size-age composition of the recreational catch off the southeastern United States. Trans. Am. Fish. Soc. 107:234-240.

MANOOCH, C. S., III, AND G. R. HUNTSMAN.

1977. Age, growth and mortality of the red porgy, *Pagrus pagrus*. Trans. Am. Fish. Soc. 106:26-33.

MUNRO, J. L., V. C. GAUT, R. THOMPSON, AND P. H. REESON.

1973. The spawning seasons of Caribbean reef fish. J. Fish Biol. 5:69-84.

MUSICK, J. A., AND J. D. MCEACHRAN.

1972. Autumn and winter occurrence of decapod crustaceans in the Chesapeake Bight, U.S.A. Crustaceana 22:190-200.

OGDEN, J. C., AND P. R. EHRLICH.

1977. The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). Mar. Biol. (Berl.) 42:273-280.

PARKER, R. O., JR., R. B. STONE, AND C. C. BUCHANAN.

1979. Artificial reefs off Murrells Inlet, South Carolina. Mar. Fish. Rev. 41(9):12-24.

POWLES, H., AND C. A. BARANS.

1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. Mar. Fish. Rev. 42(5): 21-35.

RANDALL, J. E.

1968. Caribbean reef fishes. T.F.H. Publications, Neptune City, N.J., 318 p.

REID, G. K., JR.

1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4:1-94.

RICKER, W. E.

1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

ROHR, B. A., AND E. J. GUTHERZ.

1977. Biology of offshore hake, *Merluccius albidus*, in the Gulf of Mexico. Fish. Bull., U.S. 75:147-158.

SAKSENA, V. P., AND W. J. RICHARDS.

1975. Description of eggs and larvae of laboratory-reared white grunt, *Haemulon plumieri* (Lacépède) (Pisces, Pomadasyidae). Bull. Mar. Sci. 25:523-536.

SAUSKAN, V. I., AND A. OLAECHEA.

1974. Biology and population abundance of the tomtate (*Haemulon aurolineatum*) (Cuvier and Valenciennes, 1830, Pomadasyidae, Perciformes) on Campeche Bank. [In Russ.] *In* A. S. Bogdanov (editor), Soviet-Cuban fishery research, Vol. 4, p. 135-510. Instituto de Investigación Cientifica de la Economía Pesquera Marina y de la Oceanografía de toda la Unión (VNIRO), Centro de Investigaciones Pesqueras (CIP), Mosc.

SMITH, C. L., AND J. C. TYLER.

1972. Space resource sharing in a coral reef fish community. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: Ecology of coral reef fishes, p. 125-170. Natl. Hist. Mus. Los Ang. Cty., Sci. Bull. 14.

SOKOLOVA, L. V.

1969. Distribution and biological characteristics of the main commercial fish of Campeche Bank. *In* A. S. Bogdanov (editor), Soviet-Cuban fishery research, p. 208-224. Isr. Program Sci. Transl., Jerusalem.

SPRINGER, V. G., AND K. D. WOODBURN.

1960. An ecological study of the fishes of the Tampa Bay area. Fla. Board Conserv. Mar. Lab. Prof. Pap. Ser. 1, 104 p.

STONE, R. B., H. L. PRATT, R. O. PARKER, JR., AND G. E. DAVIS.

1979. A comparison of fish populations on an artificial and natural reef in the Florida Keys. Mar. Fish. Rev. 41(9):1-11.

STRUHSAKER, P.

1969. Demersal fish resources: Composition, distribution, and commercial potential of the continental shelf stocks off southeastern United States. Fish. Ind. Res. 4:261-300.

TAYLOR, C. C.

1953. Nature of variability in trawl catches. U.S. Fish Wildl. Serv., Fish. Bull. 54:145-166.

WALFORD, L. A.

1946. A new graphic method for describing the growth of animals. Biol. Bull. (Woods Hole) 90:141-147.

WENNER, C. A., C. A. BARANS, B. W. STENDER, AND F. H. BERRY.

1979a. Results of MARMAP otter trawl investigations in the South Atlantic Bight. I. Fall 1973. S.C. Mar. Resour. Cent. Tech. Rep. 33, 79 p.

1979b. Results of MARMAP otter trawl investigations in the South Atlantic Bight. II. Spring, 1974. S.C. Mar. Resour. Cent. Tech. Rep. 40, 78 p.

1979c. Results of MARMAP otter trawl investigations in the South Atlantic Bight. III. Summer, 1974. S.C. Mar. Resour. Cent. Tech. Rep. 41, 62 p.

1979d. Results of MARMAP otter trawl investigations in the South Atlantic Bight. IV. Winter-early Spring, 1975. S.C. Mar. Resour. Cent. Tech. Rep. 44, 59 p.

WILK, S. J., AND M. J. SILVERMAN.

1976. Fish and hydrographic collections made by the research vessels *Dolphin* and *Delaware II* during 1968-72 from New York to Florida. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-697, 159 p.

GROWTH OF THE OCEAN QUAHOG, *ARCTICA ISLANDICA*, IN THE MIDDLE ATLANTIC BIGHT

STEVEN A. MURAWSKI, JOHN W. ROPES, AND FREDRIC M. SERCHUK[1]

ABSTRACT

In situ growth rate of the ocean quahog, *Arctica islandica*, was investigated at a site 53 m deep off Long Island, New York, during 1970-80. Specimens notched during summer 1978 and recaptured 1 and 2 calendar years later yielded information on shell growth and the periodicity of supposed annual marks. Growth of specimens recaptured after 1 year at liberty ($n = 67$, 59-104 mm shell length) was described by $SL_{t+1} = 2.0811 + 0.9802\ SL_t$, where SL is shell length in millimeters at age t. Average shell length of marked specimens recaptured during summer 1980 increased 1.17 mm ($n = 200$), approximately twice that of ocean quahogs recaptured in 1979 (0.56 mm). Band formation on the external surface of small ocean quahogs (less than about 60 mm) was apparently an annual event since small specimens recaptured in 1979 formed one such mark during the interval between release and recapture. Small specimens sampled during summer exhibited relatively wide marginal growth from the last external mark to the shell edge, while winter samples had formed new annuli at the shell margin, thus, external bands were formed during early autumn-early winter. Internal banding in shell cross sections of small ocean quahogs correlated in number and position with external features. An equation representing back-calculated growth, based on external banding patterns of small unmarked specimens (19-60 mm) captured during summer 1978, was: $SL = 75.68\text{-}81.31\ (0.9056)^t$, where t is age in years. Length-frequency samples were available for the vicinity of the marking study from routine dredge surveys of clam resources during 1970-80. Growth rates inferred from progressions of length-frequency modes in 1970 and 1980 samples were similar to those computed from mark-recapture and age-length equations. Ocean quahogs are apparently among the slowest growing and longest lived of the continental shelf pelecypods; annual increases in shell length were 6.3% at age 10, 0.5% at age 50, and 0.2% at an estimated age of 100 years.

Research on the population dynamics of the ocean quahog, *Arctica islandica*, has become increasingly important in recent years. An intensive fishery for the species developed off New Jersey and the Delmarva Peninsula during the mid-1970's. The resulting increases in U.S. landings were dramatic: from 588 t of shucked meats in 1975 to a record 15,748 t by 1979. Estimates of the growth rate and longevity of ocean quahogs inhabiting the Middle Atlantic Bight are necessary to assess potential impacts of various harvesting strategies on the resources (Murawski and Serchuk[2]; Mid-Atlantic Fishery Management Council[3]).

Several early studies alluded to the age and growth rate of *Arctica islandica*, yet citations were largely anecdotal and generally did not reflect critical evaluations of the rate of growth or the validity of aging criteria. Turner (1949) reported an observation by G. Thorson that "European investigators who have studied the chemical composition of the shell found reason to believe that it took six years or more for mahogany (ocean) quahaugs (quahogs) to reach average size." Loosanoff (1953) stated that ocean quahogs he examined for reproductive studies "were adults, several years old, and averaged 3½ to 4 inches (89-102 mm) in length." Jaeckel (1952) noted *Cyprina* (=*Arctica islandica*) could perhaps attain ages up to 20 "Sie kann hohes Alter (Vielleicht bis zu 20 Jahven) erreichen." Skuladottir[4] did not elaborate on aging methodologies

[1]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Murawski, S. A., and F. M. Serchuk. 1979. Distribution, size composition, and relative abundance of ocean quahog, *Arctica islandica*, populations off the Middle Atlantic Coast of the United States. ICES/C.M. 1979/K:26, Shellfish Comm., 22 p.

[3]Mid-Atlantic Fishery Management Council. 1979. Amendment No. 2 for the surf clam and ocean quahog fishery management plan and final supplemental environmental impact statement. Mid-Atlantic Fishery Management Council, Dover, Del., 114 p.

[4]Skuladottir, U. 1967. Kraffadyr og skeldyr (Crustacean and mollusks). Radstefna Isl. Verkfraedinga. 52:13-23.

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but claimed "the oldest clams were up to 18 years and about 9 cm long. The bulk was in the 10-14 year group and 7-8.7 cm long."

The external color of large ocean quahogs (greater than about 60 mm shell length) is usually solid black; however, the periostracum of small individuals is variable in color, grading from pale yellow to deep brown (Lovén 1929; Hiltz[5]). Concentric dark bands appearing in the shell surface of small specimens have thus been interpreted as annuli by several authors. Although Lovén did not present age-size relationships explicitly, he did note the presence of external "annual rings" ("Jahresringe") and presented photographs of a size range of small ocean quahogs, illustrating the relationship between numbers of rings and shell lengths. Chandler[6] measured the maximum diameters of concentric rings and derived growth relationships based on eight specimens (96 total measurements, to millimeters). The largest number of such rings appearing on an individual ocean quahog was 21; the corresponding shell length was 58.5 mm. Caddy et al.[7] presented growth curves, based on external markings, for small ocean quahogs from the Northumberland Strait and Passamaquoddy Bay. Average length at age was consistently greater for the more southern area.

Unpublished manuscripts by Chéné[8] and Meagher and Medcof[9] document efforts to more precisely establish ocean quahog growth rates. Mark and recapture experiments were conducted in Brandy Cove, New Brunswick. Notched specimens ($n = 14$), averaging 57.4 mm (shell length) when recaptured, grew an average of 0.6 mm (shell height) between September 1970 and September 1971. Sequential observations of eight small ocean quahogs (mean length 20.16 mm) was undertaken to assess growth rates and seasonal changes in the color patterns of the periostracum. These individuals were held in cages and grew an average 17% in length from 4 June to 31 August 1971. Periostracum formed during the interval was brown, contrasting with yellow material formed before the study was begun. However, this banding pattern may not have been indicative of a normally occurring annual event since "the caged clams were sensitive to experimental treatments and produced disturbance rings each time they were air-exposed for observation" (Meagher and Medcof footnote 9).

Several recent studies have examined banding patterns present in shell cross sections and have attempted to validate the hypothesis of band formation as an annual event. Jones (1980) noted that marginal increments of shell deposition beyond the last band followed a seasonal progression; bands were formed once per year between September and February. The most rapid production of shell was from late spring to early summer; annulus formation overlapped the spawning period in mature individuals. Thompson et al. (1980) presented size-frequency data of small specimens from the Baltic Sea and interpreted external and cross-sectional banding in these specimens as supporting evidence for annual periodicity of band formation in larger (older) specimens from the Middle Atlantic Bight. Thompson et al. further stated that preliminary results from radiochemical analysis of shells corroborated age analysis based on shell banding patterns.

We initiated a project during summer 1978 to assess in situ growth rates of ocean quahogs at a deepwater site off Long Island, N.Y. Objectives of the study were to obtain growth increment data directly from mark-recapture, further evaluate the potential of banding patterns (both external and in shell cross section) as indicators of age, and correlate growth measurements with a 10-yr time-series of length frequencies collected in the vicinity of the marking site. Length-weight relationships have been established for the Middle Atlantic, based on a synoptic winter survey (Murawski and Serchuk 1979); however, no data have been published on seasonal variations. An additional objective of the project was to compare winter and summer length-weight relations at the marking site.

(Proceedings of the conference of Islandic Professional Engineers. Fish. Res. Board Can., Biol. Stn., St. Andrews, N.B., Trans. Bur., No. 1206.)

[5]Hiltz, L. M. 1977. The ocean clam (*Arctica islandica*). A literature review. Fish. Mar. Serv. Tech. Branch, Halifax, N.S., Tech. Rep. 720, 177 p.

[6]Chandler, R. A. 1965. Ocean quahaug resources of Southeastern Northumberland Strait. Fish. Res. Board. Can., Manuscr. Rep. (Biol.) 828, 9 p.

[7]Caddy, J. F., R. A. Chandler, and D. G. Wildler. 1974. Biology and commercial potential of several underexploited molluscs and crustacea on the Atlantic coast of Canada. Presented at Federal-Provincial committee meeting on Utilization of Atlantic Resources, Montreal, Feb. 5-7 1974. Prepared at Fisheries Research Board of Canada, St. Andrews Biological Station, N.B.

[8]Chéné, P. L. 1970. Growth, PSP accumulation and other features of ocean clams (*Arctica islandica*). Fish. Res. Board Can., St. Andrews Biol. Stn., Orig. Manuscr. Rep. 1104, 34 p.

[9]Meagher, J. J., and J. C. Medcof. 1972. Shell rings and growth rate of ocean clams (*Arctica islandica*). Fish. Res. Board Can., St. Andrews Biol. Stn., Orig. Manuscr. Rep. 1105, 26 p.

FIELD STUDIES

Intermittent surveys of offshore clam resources of the Middle Atlantic Bight have been conducted since 1965 by the National Marine Fisheries Service, and its predecessor the Bureau of Commercial Fisheries (Merrill and Ropes 1969; Murawski and Serchuk footnote 2; Serchuk et al.[10]). Cruises were designed to yield information on temporal and areal aspects of distribution, size composition, and relative abundance of both surf clam, *Spisula solidissima*, and ocean quahog. Stations were sampled in a grid array prior to 1978; surveys from 1978 to 1980 employed a stratified-random scheme. Commercial-type hydraulic clam dredges were modified to retain small individuals and used as survey gear; dredge specifications and vessels varied somewhat among cruises (Serchuk et al. footnote 10; Table 1).

We selected an area for intensive field study of ocean quahog growth, based on an evaluation of pre-1978 survey data and knowledge of commercial fleet activities. Specific criteria were: 1) sufficient clam densities for rapid capture of individuals used in the marking experiment, 2) abundant numbers of clams over a wide size range, 3) clam densities similar to sites frequented by fishing vessels, and 4) lack of previous exploitation and low probability of near-future use. These specifications were met at a site 48 km south-southeast of Shinnecock Inlet, Long Island, at lat. 40°25.1′N, long. 72°23.7′W. Water depth was 53 m, and substrata consisted of coarse sand and shell, primarily ocean quahog and sea scallop, *Placopecten magellanicus*. Live invertebrates present in survey samples included *Lunatia heros*, *Echinarachnius parma*, *Venericardia borealis*, *Aphrodite aculeata*, and *Astarte* spp., in addition to ocean quahog and sea scallop.

Water depth at the study site precluded extended periods of bottom time using normal scuba methods, thus we elected to sample ocean quahogs with commercial and research dredging vessels. The probability of recapturing marked ocean quahogs at the site was considered to be relatively low because of water depth, width of sampling gear, difficulties in positioning the vessel at a precise location, and the accuracy of the loran-C navigation system. Hence it was decided to mark and redistribute large numbers.

Incremental increases in clam shell growth corresponding to known time durations can be measured if a point of reference is initially established at the margin of the growing shell. Growth is determined directly from recaptured specimens and shell length at marking can either be measured or back-calculated. Thus we needed only to indelibly etch the shell edge of live quahogs and return them to the sea bed, obviating the laborious and time-consuming process of measuring and number-coding individuals prior to release.

Notching techniques have been used successfully to study growth rate and to validate the periodicity of band formation in a number of bivalve species including soft shell clam, *Mya arenaria* (Mead and Barnes 1904); hard shell clam, *Mercenaria mercenaria* (Belding 1912); American oyster, *Crassostrea virginica* (Loosanoff and Nomejko 1949); sea scallop (Stevenson

[10]Serchuk, F. M., S. A. Murawski, E. M. Henderson, and B. E. Brown. 1979. The population dynamics basis for management of offshore surf clam populations in the Middle Atlantic. Proceedings of the Northeast Clam Industries - Management for the Future, Coop. Ext. Serv. Univ. Mass.-MIT Sea Grant, p. 83-101.

TABLE 1.—Characteristics of survey gear and length-frequency statistics of ocean quahogs collected near lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight, 1970-80.

Vessel	Dates	Hydraulic dredge blade width (cm)	Spacing between[1] bars or rings (mm)	Shell length (mm)			
				$\bar{X}$	SD	Range	*n*
RV *Delaware II*	13 August 1970	122	30	[2]74.1	20.1	25-105	107
RV *Delaware II*	24 April 1976	122	30	74.1	16.6	40-115	271
RV *Delaware II*	27 February 1977	122	30	73.4	14.5	45-104	234
RV *Delaware II*	1 January-2 February 1978	122	30	74.5	14.3	34-113	211
FV *Diane Maria*[3]	26 July-5 August 1978	254	13	74.5	15.4	31-112	1,262
RV *Delaware II*	9 January 1979	152	25	71.4	14.5	33-116	1,317
RV *Delaware II*[4]	14-21 August 1979	152	25-51	76.5	15.2	38-111	811
RV *Delaware II*	8 February 1980	152	51	74.2	13.8	38-117	5,546
RV *Delaware II*[4]	9 September 1980	152	51	74.8	13.4	40-108	1,899

[1]Dimension in the portion of the dredge where catch is accumulated.
[2]Samples measured to the nearest 0.5 cm.
[3]Initiation of marking study.
[4]Recapture of marked individuals.

and Dickie 1954; Merrill et al. 1966); and surf clam (Ropes and Merrill 1970; Jones et al. 1978). Accordingly, we marked ocean quahogs by cutting shallow grooves from the ventral margin up the shell surface using thin carborundum discs mounted on an electric grinder (Ropes and Merrill 1970). Two parallel grooves 2 mm apart were cut into each shell to distinguish our marks from shells scratched by natural processes or during dredging (Fig. 1).

Marking operations were conducted from 26 July to 5 August 1978 (Table 1). A total of 41,816 ocean quahogs was notched by the previously described technique. Batches of 3,000-5,000 clams were dredged from within 9 km of the planting site, marked, and redistributed. The method of marking and planting clams was rapid; about 1,600 clams were marked per hour. A grid system based on loran-C coordinates, was used to indicate the location of each batch. Length-frequency samples were obtained during the marking phase (Table 1), and 134 small ocean quahogs (19-60 mm) were retained for maturity studies and analyses of exterior and cross-sectional banding.

An intensive effort to recapture marked individuals was undertaken, 1 calendar year after planting, during 14-21 August 1979 (Table 1). Forty-three hydraulic dredge tows, each of about 5-min duration, were completed at the site. A Northstar 6000[11] loran-C set and an Epsco loran-C plotter were used in the systematic search of a 20,000 m^2 area. A total of 14,043 ocean quahogs was examined; 74 (0.5%) had been marked. Recaptured specimens were photographed, measured, and frozen intact at sea. A random sample of 126 unmarked ocean quahogs was frozen for length-weight comparison with marked individuals.

Marked individuals were again recaptured, approximately 2 yr after planting, on 9 September 1980 (Table 1). Two dredge tows yielded 1,899 ocean quahogs; 249 individuals (13.1%) had been marked.

Length-frequency measurements were obtained from the site during routine assessment surveys in January 1979 and February 1980. Sampling within 10 km of the site was historically serendipitous; catch data were available from four surveys between 1970 and February 1978 (Table 1). Lengths of ocean quahogs taken near the site exhibited a consistent bimodal frequency distribution throughout the time-series. Growth rate information from the mark-recapture and shell banding experiments was thus compared with that generated from modal progression in sequential length frequencies.

A random sample of 278 ocean quahogs taken from the site during February 1980 was frozen whole for length-weight comparison with the August 1979 sample. Small ocean quahogs (≤60 mm) were also frozen intact for analysis of the timing of periodic band formation in the shells.

LABORATORY STUDIES

Mark-Recapture

Recaptured specimens were thawed but kept moist during all phases of analysis to prevent shell cracking and disintegration of the periostracum. A total of 67 of the 74 specimens recaptured in 1979 and 200 of 249 specimens recaptured in 1980 were suitable for growth analysis; the remaining samples were either shell fragments or from quahogs obviously dead when recovered. Shells were measured to the nearest 0.01 mm, using calipers or dissecting microscope equipped with an ocular micrometer. Periostracum obscured the shell edge of most specimens and was subsequently removed from the vicinity of the mark prior to measurement. Shell lengths were obtained by pressing the periostracum against the valves with calipers.

Growth increments of recaptured ocean quahogs were determined as the linear increase in shell dimension along an imaginary line passing through the umbo and equidistant between grooves that formed the mark (Fig. 1). The linear distance between the umbo and shell edge at the mark was designed as h'; shell length at marking was computed for each quahog by:

$$SL_t = SL_{t+1} - \left[\frac{SL_{t+1}}{h'_{t+1}} \cdot (h'_{t+1} - h'_t) \right] \quad (1)$$

where SL_t = shell length (longest linear dimension) at marking,
SL_{t+1} = shell length at recapture,
h'_t = linear measurement between umbo and edge of the shell equidistance between grooves, at marking,
h'_{t+1} = linear measurement between umbo and edge of the shell

[11]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

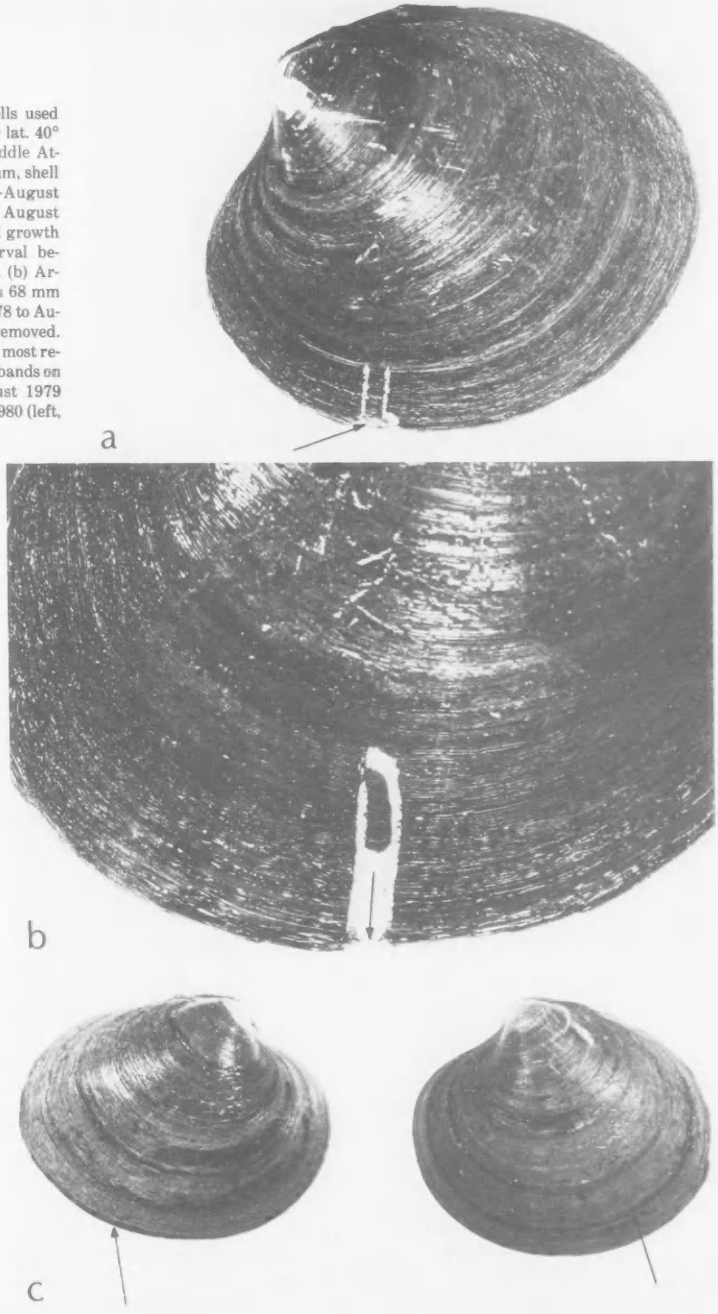

FIGURE 1.—Ocean quahog shells used for growth analyses taken near lat. 40° 25'N, long. 72°24'W, in the Middle Atlantic Bight. (a) Specimen 65 mm, shell length, marked during July-August 1978 and recaptured during August 1979. Arrow indicates external growth band formed during the interval between marking and recapture. (b) Arrow indicates shell growth of ≡ 68 mm specimen from July-August 1978 to August 1979 with periostracum removed. (c) Arrows indicate positions of most recently formed external growth bands on small individuals from August 1979 (right, 43 mm) and February 1980 (left, 45 mm) samples.

equidistant between grooves, at recapture.

Marginal growth in shell length was thus equivalent to the bracketed term.

Implicit in Equation (1) is the assumption that ratios between the linear parameters SL and h' did not change between marking and recapture (isometric growth). The assumption is supported by comparisons of various standard shell dimensions (i.e., shell length, height, and width, Chandler footnote 6; Northeast Fisheries Center Woods Hole Laboratory unpubl. data), particularly considering the relatively small percent changes in shell size between marking and recapture (Table 2).

TABLE 2.—Growth of ocean quahogs marked during August 1978, and recaptured during August 1979 (n = 67), and September 1980 (n = 200), at lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight.

Parameter	Year	Mean (mm)	SD (mm)	Range (mm)
Shell length at recovery	1979	77.31	14.67	59.12-104.40
	1980	79.01	13.91	57.69-103.66
Calculated growth increment in shell length	1979	0.56	0.38	0.08-1.38
	1980	1.17	1.04	0.07-4.32
Calculated shell length at marking	1979	76.76	14.97	58.15-104.09
	1980	77.84	14.75	55.46-103.43

Three methods were used to fit growth equations to mark-recapture data. For ocean quahogs recovered 1 calendar year after marking, length at recapture was related to length at marking using Ford-Walford and linear annual increment plots described by Gulland (1969; Fig. 2). Additionally, a nonlinear exponential equation was fit to increment data and results compared with those assuming the von Bertalanffy model. The von Bertalanffy parameters L_∞ and K were also estimated using the BGC4 computer program (Abramson 1971). The program was designed for determining growth parameters when lengths of unaged individuals are known at two points in time, based on the algorithm of Fabens (1965).

Equations derived from mark-recapture data can be used to describe relative growth from an arbitrary point in time (i.e., SL_{t+1}, SL_{t+2}, ... SL_{t+n}), but without at least one independently derived age-length observation, absolute growth curves cannot be established. Accordingly, analyses of external banding patterns of small ocean quahogs were critical in "fixing" growth curves from mark-recapture.

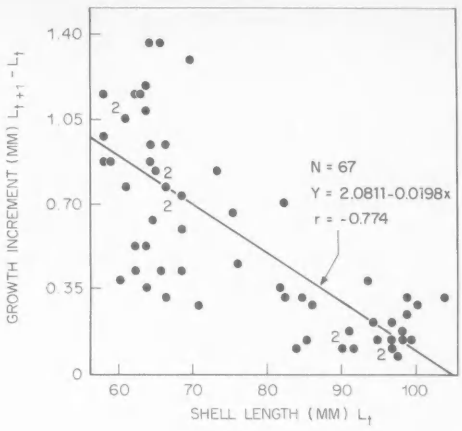

FIGURE 2.—Relation between calculated increment of growth in shell length (millimeters) and initial length for ocean quahogs marked during July-August 1978 and recaptured during August 1979 near lat. 40°25′N, long. 72°24′W, in the Middle Atlantic Bight.

Shell Banding

Small ocean quahogs retained from the July-August 1978 cruise were analyzed for external and internal shell banding patterns. Sequential growth of individual ocean quahogs was followed by measuring the maximum dimension (shell length) of exterior bands appearing on the periostracum, using calipers (Fig. 1). Maximum shell length beyond the last band was also recorded. The opposite valve was sectioned from the umbo to the ventral margin and polished (Saloman and Taylor 1969; Jones et al. 1978). An acetate impression of the polished surface was made and mounted between glass slides. Images were enlarged with a microprojector to reveal internal banding patterns.

Internal lines present in shell cross sections correlated in number and position with external bands when the latter were distinct. The periostracum on some shells was eroded near the umbo, obscuring external bands. In these cases "annuli" nearest the umbo were located on the peels, but measurements of shell size could not be made (Table 3). External marks present near the shell margins on some larger specimens also could not be discerned; internal banding was again used to estimate age. Shell length statistics were computed for each age/annulus subclass, weighted lengths at annuli for all ages and

TABLE 3.—Back-calculated growth (shell length, in millimeters) of small ocean quahogs. Samples taken from lat. 40°25′ N, long. 72°24′ W, 26-29 July 1978, in the Middle Atlantic Bight.

Number of annuli		Length at capture	Length at annulus												
			1	2	3	4	5	6	7	8	9	10	11	12	13
2	$\bar{x}$	18.00	7.00	12.30											
	SD	0.00	0.00	0.00											
	n	1	1	1											
3	$\bar{x}$	23.36	4.59	10.59	18.01										
	SD	3.42	0.78	2.66	3.14										
	n	9	9	9	9										
4	$\bar{x}$	29.73	4.39	10.04	16.99	24.38									
	SD	2.00	0.73	2.13	2.38	1.96									
	n	14	14	14	14	14									
5	$\bar{x}$	34.58	4.43	8.80	14.45	21.72	29.72								
	SD	3.19	0.07	1.50	2.29	3.08	3.41								
	n	26	26	26	26	26	26								
6	$\bar{x}$	38.49	4.07	7.77	13.40	19.13	26.09	33.88							
	SD	2.73	0.59	1.57	2.49	2.58	2.73	2.92							
	n	27	[1]25	27	27	27	27	27							
7	$\bar{x}$	41.66	4.16	7.66	12.10	17.42	23.87	30.81	37.61						
	SD	2.00	1.10	1.34	1.72	1.57	1.87	1.98	2.05						
	n	29	[1]27	29	29	29	29	29	29						
8	$\bar{x}$	46.24	3.92	7.59	12.29	16.92	23.64	29.95	36.63	42.76					
	SD	1.78	0.98	1.44	2.39	2.77	2.38	2.52	2.22	1.99					
	n	10	10	10	10	10	10	10	10	10					
9	$\bar{x}$	47.60	3.10	7.50	11.00	15.90	21.30	27.40	33.50	39.20	44.90				
	SD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
	n	1	1	1	1	1	1	1	1	1	1				
10	$\bar{x}$	48.23	3.67	6.47	11.77	15.97	20.80	25.57	31.17	36.90	40.40	45.30			
	SD	0.59	0.29	0.50	1.19	2.48	2.31	2.35	1.89	2.07	0.36	0.30			
	n	3	3	3	3	3	3	3	3	3	3	3			
11	$\bar{x}$	54.35	3.90	5.70	9.35	13.80	20.30	27.60	34.20	40.20	44.45	48.50	51.95		
	SD	2.05	0.00	0.42	0.78	0.28	3.68	4.81	2.83	1.41	1.06	0.71	1.20		
	n	2	[1]1	2	2	2	2	2	2	2	2	2	2		
12	$\bar{x}$	53.87	3.73	7.23	10.07	12.97	19.13	27.00	31.60	35.67	39.50	43.50	44.75	49.55	
	SD	3.95	0.35	1.38	2.30	3.28	4.15	9.37	8.56	7.90	8.42	8.23	1.91	2.90	
	n	3	3	3	3	3	3	3	3	3	3	3	[2]2	2	
13	$\bar{x}$	53.90	—	5.20	9.70	12.80	17.50	22.20	28.00	34.70	38.30	43.70	46.40	50.00	52.00
	SD	0.00	—	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	n	1	[1] —	1	1	1	1	1	1	1	1	1	1	1	1
14[2]	$\bar{x}$	51.15	3.85	7.30	10.65	15.30	22.40	29.10	33.75	38.75	43.40	48.10			
	SD	5.16	0.50	2.26	2.19	0.42	0.57	1.56	1.34	0.07	1.98	0.00			
	n	2	2	2	2	2	2	2	2	2	2	1			
16[2]	$\bar{x}$	57.93	4.00	6.95	12.05	18.50	24.80	31.53	37.25	42.60	46.57	50.30	55.30		
	SD	2.90	0.00	1.11	2.24	2.49	3.95	3.75	2.91	2.60	1.59	1.84	0.00		
	n	4	[1]2	4	4	4	4	4	4	4	3	2	1		
18[2]	$\bar{x}$	57.10	3.60	7.55	10.95	16.40	24.60	29.85	40.10	43.40	46.80	49.00			
	SD	0.99	0.00	2.05	3.89	5.80	5.37	4.46	0.00	0.00	0.00	0.00			
	n	2	[1]1	2	2	2	2	2	1	1	1	1			
ALL	$\bar{x}$	38.94	4.21	8.27	13.59	19.17	25.44	31.13	36.28	40.40	42.82	46.52	49.18	49.70	52.00
	SD	8.65	0.85	1.95	3.03	3.69	3.95	3.75	3.47	4.01	4.41	4.32	4.58	2.07	0.00
	n	134	125	134	133	124	110	83	56	27	16	13	6	3	1
	Min	18.7	2.5	5.1	7.8	9.3	14.5	18.6	24.5	29.3	32.4	36.0	43.4	47.5	52.0
	Max	60.4	7.0	15.8	22.5	26.7	36.4	38.1	41.9	46.2	48.8	52.3	55.3	51.6	52.0

[1]External mark eroded but mark present in shell cross section.
[2]Number of annuli exceeds the number of lengths at annulus because marks could be distinguished in shell cross sections that were too closely spaced to discern on shell surfaces.

lengths at capture were also determined (Table 3).

Specimens recaptured in 1979 ranged in shell length from 59 to 104 mm, most had a deep brown or black periostracum. Several specimens did, however, exhibit the characteristic external banding pattern (Fig. 1), and were useful in validating the presumed annual periodicity of marks.

Marginal shell growth beyond the last external mark was strikingly different among small ocean quahogs from August 1979 and February 1980 samples. Mean lengths at capture for individual age classes from summer 1978 (particularly ages 1-9) were substantially greater than lengths at the last annulus, and were nearly equivalent to mean lengths at the last annulus for the next age class (Table 3). Ocean quahogs from winter 1980 invariably had formed or were forming an annulus at the shell margin (Fig. 1). A similar pattern was noted in shell cross sections.

Modified exponential and logistic growth equations were fitted to mean back-calculated lengths at age, from the July 1978 samples (Table 3), using the asymptotic regression and nonlinear least squares computer programs BMDO6R and BMDO7R, respectively (Dixon 1977; Fig., 3). Few aged shells were as large as those recaptured (Tables 2, 3). Growth functions generated from aging data were thus extrapolated to the size range of recaptured specimens and results compared with annual growth increments predicted from mark-recapture (Figs. 2, 3). An age-size point necessary to initiate the mark-recapture growth function was computed from growth equations fitted to age-length data generated in shell banding experiments; the mark-recapture equation was then iterated to encompass most shell lengths present at the marking site (Figs. 4, 5).

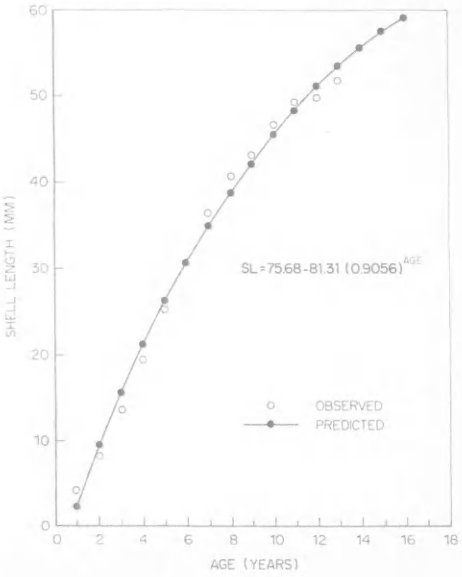

FIGURE 3.—Observed and predicted shell lengths at age for small ocean quahogs sampled during July 1978 near lat. 40°25′ N, long. 72°24′W, in the Middle Atlantic Bight.

Length-Weight

Shell length-drained meat weight relationships were computed for samples taken during August 1979 and February 1980. Laboratory

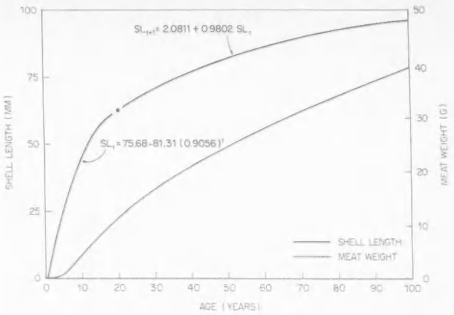

FIGURE 4.—Predicted shell lengths (millimeters) and drained meat weights (grams) at age for ocean quahogs at lat. 40°25′ N, long. 72°24′W, in the Middle Atlantic Bight. Growth in length is described by an equation derived from studies of external banding patterns of small individuals (left of dot), and the Ford-Walford equation from mark-recapture data (right of dot). Weights at age are derived by applying the overall length-weight equation presented in Table 5 to calculated mean lengths at age.

and statistical methods are given in Murawski and Serchuk (1979). Equations for recaptured and unmarked specimens from August 1979 were compared by covariance analysis to assess effects of marking (Table 4). Presumably, if physiological processes of the animal were significantly disrupted by the marking procedures, the adjusted mean of the length-weight equation might be statistically lower than that of controls. Seasonal variability in length-weight was investigated by comparing summer and winter equations (Table 5).

RESULTS AND DISCUSSION

New shell growth of recaptured individuals was clearly discernible in small specimens (<70 mm) not only at the mark, but all along the

TABLE 4.—Ocean quahog shell length-meat weight regression equations, and analysis of covariance for marked and unmarked individuals sampled at lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight, during August 1979.

	Linear regression parameters			
Sample	Intercept (*a*)	Slope (*b*)	*r*	*n*
Marked	−9.8373	2.9530	0.975	55
Unmarked	−9.0170	2.7637	0.953	126

	Test of adjusted mean			Test of slope	
Sample	Adjusted mean	df	*F*	df	*F*
Marked	2.8702	1,178	0.001 n.s.	1,177	2.13 n.s.
Unmarked	2.8714				

n.s. = $P>0.05$.

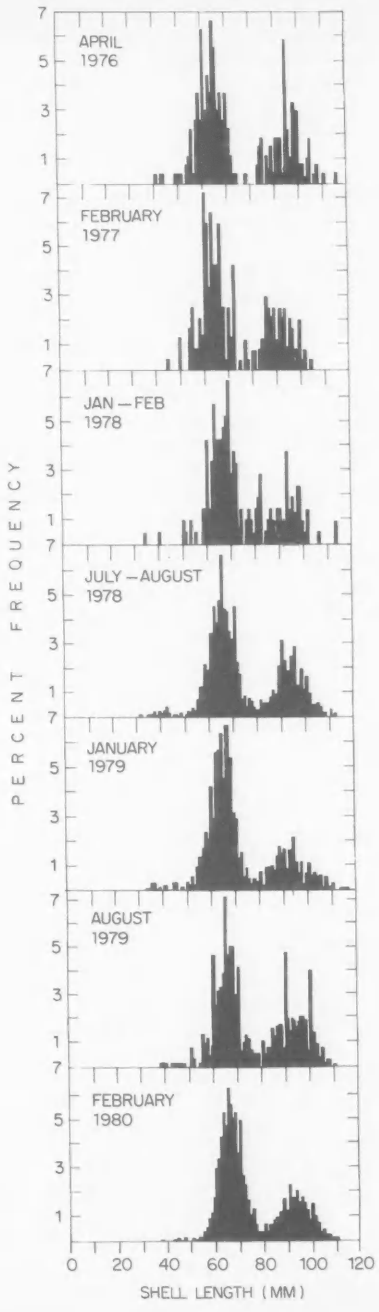

FIGURE 5.—Length-frequency distributions (1 mm intervals) of ocean quahogs sampled near lat. 40°25′N, long. 72°24′W, in the Middle Atlantic Bight, April 1976-February 1980.

TABLE 5.—Ocean quahog shell length-meat weight regression equations, and analysis of covariance for August 1979 and February 1980 samples taken near lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight.

Sample	Linear regression parameters			
	Intercept (*a*)	Slope (*b*)	*r*	*n*
August 1979	−9.2901	2.8274	0.961	181
February 1980	−8.6865	2.7086	0.976	278
All data	−9.0627	2.7871	0.967	459

Sample	Test of adjusted mean			Test of slope	
	Adjusted mean	df	*F*	df	*F*
February 1980	3.0302	1,456	58.86**	1,455	3.22 n.s.
August 1979	2.9398				

**$P \leq 0.01$; n.s. = $P > 0.05$.

ventral margin when the periostracum was removed (Fig. 1). A growth interruption was produced at the previous shell edge of small specimens; new material was formed slightly below the earlier shell margin and was shinglelike in appearance (Fig. 1). Growth in larger ocean quahogs was less distinct and thus more difficult to measure. Where clear growth interruptions were not present, a faint yellowish band contrasting with white shell material was interpreted as a marking-induced check and growth was measured from that point. Shell growth was assessed midway between grooves that formed the mark since, in the case of larger specimens, the depth of the grooves was actually greater than the amount of new shell deposited (Figs. 1, 2).

A total of 11,658 ocean quahogs was measured directly from dredge catches at the marking site during 1970-80 (Table 1; Figs. 5, 6). Although minimum spacing of bars or rings in the rear portion of dredges varied somewhat (Table 1), size selectivity was apparently not significantly altered. Repeated tows were made at the marking site during August 1979 with 25 × 25 mm and later 51 × 51 mm wire mesh in the after portion of the dredge. Size distributions of ocean quahogs were nearly identical before and after the alteration. A possible explanation for the lack of differential selectivity is that shell, sand, and live invertebrates may have clogged the dredge at the beginning of tows, negating further filtering ability.

Two discrete length-frequency modes were exhibited in all sets of samples (Figs. 5, 6). Few small ocean quahogs (<50 mm) were encoun-

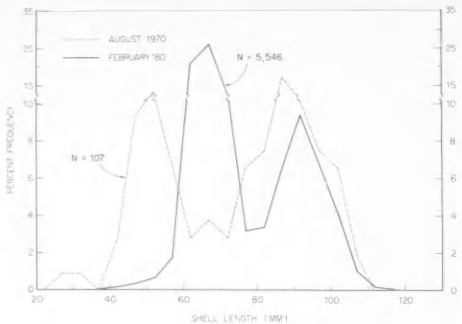

FIGURE 6.—Length-frequency distributions (5 mm intervals) of ocean quahogs sampled near lat. 40°25′N, long. 72°24′W, in the Middle Atlantic Bight, August 1970 and February 1980.

tered from 1976 to 1980 (Fig. 5) and, considering uniformity of modes over time, recruitment was probably equally poor during 1971-76. Thus, corresponding modes in the 1970 and 1980 samples were probably composed of the same year classes (Fig. 6). Average size of the small mode increased about 13 mm during the 9½-yr interval between August 1970 and February 1980, while the large group shifted about 3 mm (Figs. 5, 6; Table 1). Size progression of modes was minimal during 1976-80; intersample variation may be primarily related to differential sample sizes (Table 1). The effects of a sevenfold increase in sampling intensity can be seen by comparing August 1979 and February 1980 frequencies. Modes are smoothed in the latter sample, yet respective peaks are at precisely the same 1 mm intervals in both (65 and 90 mm). Average shell sizes ranged from 71 to 77 mm; however, trends in shell length among samples were not apparent (Table 1).

The average lengths of recaptured ocean quahogs (Table 2) were slightly greater than concurrent length-frequency samples (Table 1), although length extremes of the marked individuals were not as great. Recaptured ocean quahogs also exhibited the bimodal length-frequency distribution (Fig. 2), indicating recaptured specimens represented a relatively unbiased sample of marked individuals and the ocean quahog population in the immediate vicinity of the study area. Calculated increments of shell growth from ocean quahogs recaptured in 1979 ranged from 0.08 to 1.38 mm, and averaged 0.56 mm (Table 2). Those recaptured in 1980 grew an average of 1.17 mm (range 0.07-4.32 mm). Thus, incremental growth approximately doubled between summer 1979 and summer 1980, implying growth rates were similar during the 2 yr of the experiment and that marking procedures probably did not significantly disrupt growth patterns. Growth increments of ocean quahogs at liberty 1 yr generally declined with increasing shell length, although there was substantial variation about a linear fit (Fig. 2). The linear equation for predicting annual increment of growth from initial length is given in Figure 2; the Ford-Walford equation is: $SL_{t+1} = 2.0811 + 0.9802\ SL_t$, where SL is shell length (in millimeters) at age t. An exponential equation fitted to data in Figure 2 ($Y = 14.1216$ (exp $(-0.0459X)$)) explained about 8% more of the residual variance about the predicted line than did the linear equation. However, growth rates implied from length-frequency analyses were substantially greater than those from the exponential fit, and were similar to rates computed from the linear (von Bertalanffy) model. Thus, the latter model was considered more valid. Estimates of the asymptotic length (L_∞) and growth coefficient (K) from two fitting methods are:

	BGC4	*Annual increment*
L_∞ (mm)	107.06	104.95
K	0.0195	0.0200

Values of L_∞ from the two methods are >99.5% (BGC4) and 98.5% (annual increment) of the cumulative 1980 length-frequency distribution at the study site. Estimates of K are relatively low and characteristic of slow-growing, long-lived species (Beverton and Holt 1959).

Analyses of shell banding features present in small specimens indicate both external and internal marks are produced once during the biological year in these sizes. Several of the small recaptured ocean quahogs exhibited concentric external rings, and these specimens formed one such band during the interval between marking and recapture (Fig. 1a). Studies of small unmarked individuals retained from summer and winter sampling demonstrate that external and internal marks generally correspond in number and position. Internal marks were particularly useful in age determination when external marks were eroded near the umbo or closely spaced at the shell margin. Small ocean quahogs captured during the summer exhibited wide

marginal increments of shell growth from the last external and internal marks to the shell edge, whereas winter samples had recently formed annuli (Fig. 1c; Table 3). Thus, mark formation probably occurs during the last half of the calendar year. These observations are consistent with data presented by Jones (1980). In a study of the seasonality of incremental shell growth, he noted that internal growth bands in shell cross sections were formed from September to February. The formation of growth bands apparently overlaps the spawning period (Jones 1980); however, both events may be related to other physiological or environmental stimuli since specimens that were reproductively immature formed bands concurrently with mature ocean quahogs.

Back-calculated mean lengths at age varied considerably depending on the subset of data analyzed in Table 3. Mean lengths at age for all year classes (bottom rows in Table 3) were generally smaller than mean lengths at the last complete annulus (rightmost diagonal vector), and growth of recent age groups (2-8) appeared more rapid than for older ocean quahogs (Lee's phenomenon; see Ricker 1969). However, conclusions regarding the growth of older age groups (9-18) are tenuous due to the relatively small numbers of these ages sampled (87% of the samples were ≤8-yr-old).

Age analyses were limited to ocean quahogs that exhibited suitable contrast on the shell surface to discern external concentric rings. Thus, the oldest aged ocean quahogs (particularly ages 14-18) may represent the smallest, slowest growing individuals of their year classes; faster growing individuals may have reached sizes associated with color changes of the periostracum. Nevertheless, back-calculated mean lengths at age for 14- to 18-yr-old ocean quahogs did not tend to be progressively smaller than means for ages 9-13, perhaps indicating that size selectivity of older individuals was not a significant bias (Table 3).

The objectives of fitting statistical models to age-length data were to describe growth during the juvenile and early adult phases of life, and more importantly, to predict ages associated with the lengths of the smallest recaptured specimens (59-65 mm) thereby linking the age-length data and mark-recapture results into a continuous growth function. Recognizing the disparate nature of data subsets in Table 3, a series of exponential and logistic growth equations were fitted to: 1) weighted mean back-calculated lengths at age for all quahogs, 2) weighted mean lengths at age for ages 2-8, and 3) mean lengths at the last completed annuli (rightmost diagonal vector) for ages 2-10 and 2-13. For our purposes, the applicability of a particular model fit was judged not only by the total amount of variance between length and age explained by the equation, but by predicted annual growth increments in the 59-65 mm range. An appropriate model would fit as much of the age-sample data as possible and yield calculated annual growth increments consistent with those observed from recaptured specimens.

Exponential equations utilizing weighted mean back-calculated lengths for ages 2-8, and lengths at the last complete annulus for ages 2-13 yielded unacceptable fits by our criteria. The former equation was calculated with information from the linear portion of the growth curve, predicted lengths beyond age 8 were unrealistically high. The latter equation incorporated one negative growth increment (between ages 11 and 12) and thus the calculated asymptote was only 62.8 mm; predicted annual growth near the asymptote was considerably less than observed increments for that size (Fig. 2).

The logistic growth equation fitted to weighted mean lengths at age for all ocean quahogs ($SL = 52.09/1 + \exp(2.4722 - 0.4702(t))$) was superior to the respective exponential fit considering the residual sums of squares criterion. The reverse was true for the logistic equation describing mean lengths at the last annulus for ages 2-10 ($SL = 43.12/1 + \exp(2.9361 - 0.8069\ (t))$). However, asymptotic lengths were, for both logistic equations, well below the range of shell lengths considered in the mark-recapture experiments. Thus, extrapolation of logistic age-length relationships, necessary for initializing the Ford-Walford equation, was not feasible. On the contrary, the two exponential equations yielded reasonable asymptotic lengths and adequately described ocean quahog growth relative to that inferred from modal progressions in 1970 and 1980 length-frequency distributions (Fig. 6) and observed growth increments (Fig. 2).

Exponential growth equations computed from weighted mean lengths at age for all ocean quahogs and mean lengths at the last annulus for ages 2-10 were: $SL = 75.68\text{-}81.31\ (0.9056)^t$ and $SL = 72.70\text{-}75.22\ (0.8935)^t$, respectively. Mean lengths at age predicted from the two equations generally reflect differences among data sets

over the range of shell sizes used to fit the functions; however, estimated lengths at age converge near the sizes of the smallest recaptured specimens. Estimated lengths at age 20 were 64.49 and 64.29 mm, respectively. Corresponding growth increments from age 20-21 were 1.06 and 0.84 mm, well within the range of observed growth for those sizes (Fig. 2). If calculated lengths at age 20 are assumed to be the starting points for the Ford-Walford equation ($SL_{t+1} = 2.0811 + 0.9802\ SL_t$), the two acceptable exponential equations yield virtually identical growth curves when the Ford-Walford relationship is iterated. Additional growth analyses were conducted using the regression equation fitted to weighted mean back-calculated lengths for all ages because the maximum amount of information was used and the equation's behavior in the vicinity of marking data was consistent with empirical observations. However, further research on the growth patterns of small ocean quahogs is indicated in order to resolve differences between various data subsets in Table 3 and thus to define a more appropriate growth model for these sizes.

A composite growth curve incorporating the aged samples and mark-recapture data is given in Figure 4. The Ford-Walford equation was iterated to age 100 and a predicted shell length of 96.91 mm. Although ocean quahogs reach a size of at least 117 mm in the vicinity of the marking site (Table 1), ages substantially in excess of 100 are not necessarily implied because of the statistical variability in the marking data used to fit the predictor (Fig. 2). Annual growth in shell length is rapid during the first 20 yr of life, but declines significantly thereafter. Average yearly shell growth is 6.3% at age 10, 0.5% at age 50, and 0.2% at age 100.

Estimates of the von Bertalanffy parameter t_0 (age at zero length) were computed as −27.29 yr and −27.62 yr for the BGC4 and annual increment equations respectively, with $SL_{20} = 64.49$ mm (Gulland 1969, equation 3.5). Although predicted lengths at ages >20 are similar to those in Figure 4, a relatively poor fit to younger ages results from both von Bertalanffy equations.

The validity of using the age-length functions given in Figure 4 to describe ocean quahog growth at the marking site can be assessed by comparing predicted growth to that from modal progressions in length-frequency samples. Frequency distributions from 1976 to 1980 exhibit inter-sample variability in the position of major modes but no progressive shifts are discernible (Fig. 5). However, expected growth during the 5-yr period (Fig. 4) was smaller than could probably be identified, given the precision of length-frequency sampling (Table 1; Fig. 5). Length modes can be used to compute growth at the site between August 1970 and February 1980 (Fig. 6). Average growth of the smaller mode (52 mm in 1970) was about 13 mm, and the larger mode (87 mm in 1970) added about 3 mm shell length during the 9½-yr interval (Figs. 5, 6). Ocean quahogs 52 mm in length are about 12-yr-old and average 21-yr-old at 65 mm; the estimated age of 87 mm individuals is 60 yr and 90 mm quahogs average 70-yr-old (Figs. 3, 4). Thus, predicted growth during the period 1970-80 is strikingly similar to that inferred from length mode progressions, implying that age analyses and mark-recapture data adequately describe historical ocean quahog growth at the site.

The age-length relationships presented herein have been computed for shell sizes in excess of 95 mm and ages up to 100 yr. However, computed relationships for large sizes (>65 mm) are based on average growth rates from mark-recapture results and not from aging of individual specimens. It is likely, based on these analyses, that ocean quahogs do reach 100 yr in age; however, direct age determination of large individuals is contingent upon development and validation of suitable methodologies. Internal banding patterns present in shell cross sections were useful in aging small specimens since formation of the bands apparently occurs once annually. Seasonal shell formation patterns (Jones 1980) and age analyses of large individuals based on internal banding (Thompson et al. 1980; Jones 1980) are generally consistent with our data. Analysis of shell cross sections of large recaptured specimens may be useful in determining the periodicity of internal banding and the validity of the aging technique for large ocean quahogs; study of this material continues.

The regressions of shell length vs. drained meat weight for marked and unmarked ocean quahogs taken during August 1979 were not significantly different in slope or adjusted mean (Table 4). If in fact soft-tissue robustness is a valid index of relative condition, then marked individuals apparently suffered no lasting effects from the stress of dredging and handling. This observation is supported by the conclusions that incremental shell growth of marked specimens was similar to that computed from progressive

length frequencies of the population as a whole, and growth rates of marked individuals were nearly equal between 1978-79 and 1979-80.

Length-weight equations from February 1980 and August 1979 were parallel (Table 5); winter samples were apparently heavier in drained meat weight at a given shell length than summer samples. However, the magnitude of predicted differences in weight at length was small (4-11% for 65-115 mm ocean quahogs). Differences may be related to weight changes associated with sexual development, or merely a statistical artifact. Samples from winter and summer were combined to predict average weight for a given length during the year (Table 5). The resulting length-weight equation was applied to computed lengths at age to derive an age-weight relationship (Fig. 4). Initial weight gains are proportionally greater than concomitant length increases, but growth rates are nearly identical at the oldest predicted ages. Average annual increases in drained meat weight are 18.1% at age 10, 1.6% at age 50, and 0.2% at age 100 (Fig. 4).

Growth rates determined from the examination of concentric external banding patterns indicate small ocean quahogs may grow faster off Long Island than in the Northumberland Strait and in Passamaquoddy Bay (Caddy et al. footnote 7). However, data are insufficient to conclude that a latitudinal cline in ocean quahog growth exists. Factors influencing growth rates in a particular area are speculative; however, density dependence must be considered. Murawski and Serchuk (footnote 2) noted relative population stability and poor recruitment for ocean quahogs in the Middle Atlantic during 1965-77. Stable population size, poor recruitment, and slow growth are characteristic of populations under density dependent regulation. Investigation of ocean quahog growth rates at various densities may help to elucidate their interrelationship and indicate the population consequences of cropping high density areas.

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LITERATURE CITED

ABRAMSON, N. J. (compiler).
1971. Computer programs for fish stock assessment. FAO Fish. Tech. Pap. 101, 149 p.

BELDING, D. L.
1912. A report upon the quahaug and oyster fisheries of Massachusetts. Commonw. Mass., Boston, 134 p.

BEVERTON, R. J. H., AND S. J. HOLT.
1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Ciba Found. Colloq. Ageing 5: 142-180.

DIXON, W. J. (editor).
1977. BMD Biomedical computer programs. Univ. Calif. Press, Berkeley, 773 p.

FABENS, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265-289.

GULLAND, J. A.
1969. Manual of methods for fish stock assessment. Part I. Fish population analysis. FAO Man. Fish. Sci. 4, 154 p.

JAECKEL, S., jun.
1952. Zur oekologie der Molluskenfauna in der Westlichen Ostee. Schr. Naturwiss. Ver. Schleswig-Holstein 26:18-50.

JONES, D. S.
1980. Annual cycle of shell growth increment formation in two continental shelf bivalves and its paleoecologic significance. Paleobiology 6:331-340.

JONES, D. S., I. THOMPSON, AND W. AMBROSE.
1978. Age and growth rate determinations for the Atlantic surf clam, *Spisula solidissima* (Bivalvia: Mactracea), based on internal growth lines in shell cross-sections. Mar. Biol. (Berl.) 47:63-70.

LOOSANOFF, V. L.
1953. Reproductive cycle in *Cyprina islandica*. Biol. Bull. (Woods Hole) 104:146-155.

LOOSANOFF, V. L., AND C. A. NOMEJKO.
1949. Growth of oysters, *O. virginica*, during different months. Biol. Bull. (Woods Hole) 97:82-94.

LOVÉN, P. M.
1929. Bieträge zur Kenntnis der *Cyprina islandica L.* im Öresund. K. Fysiogr. Sällsk. Lund Handl. N.F. 41: 1-38. (Contribution to the knowledge of *Cyprina islandica L.* in the Öresund, Transl. Lang. Serv. Div., Off. Int. Fish., U.S. Dep. Commer., NMFS, Wash., D.C.)

MEAD, A. D., AND E. W. BARNES.
1904. Observations on the soft-shell clams. Thirty-fourth Annu. Rep. Comm. Inland Fish., R.I., p. 26-28.

MERRILL, A. S., J. A. POSGAY, AND F. E. NICHY.
1966. Annual marks on shell and ligament of sea scallop, *Placopecten magellanicus*. U.S. Fish Wildl. Serv., Fish. Bull. 65:299-311.

MERRILL, A. S., AND J. W. ROPES.
1969. The general distribution of the surf clam and ocean quahog. Proc. Natl. Shellfish. Assoc. 59:40-45.

MURAWSKI, S. A., AND F. M. SERCHUK.
1979. Shell length—meat weight relationships of ocean

quahogs, *Arctica islandica*, from the Middle Atlantic Shelf. Proc. Natl. Shellfish. Assoc. 69:40-46.

RICKER, W. E.
1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish Res. Board Can. 26:479-541.

ROPES, J. W., AND A. S. MERRILL.
1970. Marking surf clams. Proc. Natl. Shellfish. Assoc. 60:99-106.

SALOMAN, C. H., AND J. L. TAYLOR.
1969. Age and growth of large southern quahogs from a Florida Estuary. Proc. Natl. Shellfish. Assoc. 59:46-51.

STEVENSON, J. A., AND L. M. DICKIE.
1954. Annual growth rings and rate of growth of giant scallop, *Placopecten magellanicus* (Gmelin) in the Digby area of the Bay of Fundy. J. Fish. Res. Board Can. 11:660-671.

THOMPSON, I., D. S. JONES, AND D. DREIBELBIS.
1980. Annual internal growth banding and life history of the ocean quahog, *Arctica islandica* (Mollusca: Bivalvia). Mar. Biol. (Berl.) 57:25-34.

TURNER, H. J., JR.
1949. The mahogany quahaug resources of Massachusetts. *In* Report on investigations of improving the shellfish resources of Massachusetts, p. 12-16. Commonw. Mass., Dep. Conserv., Div. Mar. Fish.

LARVAL DEVELOPMENT OF *CITHARICHTHYS CORNUTUS*, *C. GYMNORHINUS*, *C. SPILOPTERUS*, AND *ETROPUS CROSSOTUS* (BOTHIDAE), WITH NOTES ON LARVAL OCCURRENCE[1, 2]

JOHN W. TUCKER, JR.[3]

ABSTRACT

Developmental series of 4 of the 12 species of *Citharichthys* and *Etropus* known from the western North Atlantic and Gulf of Mexico are illustrated and described. The series consist of *C. cornutus* (preflexion to nearly transformed, 2.2-17.4 mm body length, BL), *C. gymnorhinus* (preflexion to late transformation, 4.4-12.9 mm BL), *C. spilopterus* (preflexion to juvenile, 3.7-25.4 mm BL), and *E. crossotus* (preflexion to nearly transformed, 4.6-10.8 mm BL).

Data from this study and that for 2 species previously described permit identification of larvae of 6 of the 12 species. For the species investigated, caudal fin formula (4-5-4-4) is the most reliable indicator for the group of genera *Citharichthys*, *Cyclopsetta*, *Etropus*, and *Syacium*. Number of elongate dorsal rays, degree of cephalic spination, and pigmentation are most useful for determining genus for known forms. Number of elongate dorsal rays, number of caudal vertebrae, pigmentation, morphology, and number of gill rakers are most useful for identification of *Citharichthys* and *Etropus* larvae that have been described.

Citharichthys cornutus larvae have no pectoral melanophore, little notochordal pigmentation, heavy lateral pigmentation, 3 elongate dorsal rays, and develop 6 left pelvic rays and 25-26 caudal vertebrae. Flexion is complete at 9-10 mm SL and transformation at about 18 mm SL. Larvae have been collected during all seasons. Caudal fin development in *C. cornutus* is typical of the four species described here. *Citharichthys gymnorhinus* larvae have no pectoral melanophore, little notochordal pigmentation, light lateral pigmentation except for a caudal band, 3 elongate dorsal rays, and develop only 5 left pelvic rays and 23-24 caudal vertebrae. Flexion is complete at 7-8 mm SL and transformation probably at about 18 mm SL. Larvae have been collected during all seasons. *Citharichthys spilopterus* larvae have no pectoral melanophore, little notochordal pigmentation, light lateral pigmentation, a blunt snout, a deep body, 2 elongate dorsal rays, and develop 6 left pelvic rays and 23-24 (rarely 25) caudal vertebrae. Flexion is complete at 7-8 mm SL and transformation at 9-11 mm SL. Larvae have been collected from September through April. *Etropus crossotus* larvae have a melanophore at the base of the pectoral fin, heavy notochordal pigmentation, heavy lateral pigmentation, 2 elongate dorsal rays, and develop 6 left pelvic rays and 25-26 (very rarely 24) caudal vertebrae. Flexion is complete at 9-10 mm SL and transformation at 10-12 mm SL. Larvae have been collected in May and August and probably occur from March to August.

Twelve species of the flatfish genera *Citharichthys* and *Etropus* (subfamily Paralichthyinae, family Bothidae) are recognized from the western North Atlantic (Table 1). Because of their small size at maturity, these fishes are presently used only by the pet food and fish meal industries (Topp and Hoff 1972). However, the abundance of larvae (Richardson and Joseph 1973; Smith et al. 1975; Dowd 1978) and adults (Dawson 1969; Topp and Hoff 1972; Christmas and Waller 1973) indicates that some species may represent significant components of estuarine and marine food webs.

Larvae in the *Citharichthys-Etropus* complex are difficult to distinguish and are often ignored or classified as "unidentified bothids" in species composition analyses (e.g., Fahay 1975). Of the 12 western North Atlantic species, only *C. arctifrons* and *E. microstomus* have been described in detail (Richardson and Joseph 1973). *Citharichthys cornutus*, *C. gymnorhinus*, *C. macrops*, and *E. rimosus* have been briefly described by Dowd (1978). Larvae of the remaining species have not been reported previously. Hsiao (1940) mis-

[1]Contribution No. 1037, Virginia Institute of Marine Science, Gloucester Point, VA 23062.

[2]Derived from a thesis submitted to North Carolina State University in partial fulfillment of the requirements for the Master of Science degree.

[3]School of Marine Science of the College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, VA 23062.

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takenly described *Bothus* sp. larvae as *E. crossotus*.

In this paper I present descriptions of larvae of *C. cornutus*, *C. gymnorhinus*, *C. spilopterus*, and *E. crossotus* and summarize data useful for identifying *Citharichthys* and *Etropus* larvae.

MATERIALS AND METHODS

Abbreviations

The following institutional abbreviations are used: CP&L = Carolina Power and Light Company, Raleigh, N.C.; GCRL = Gulf Coast Research Laboratory, Ocean Springs, Miss.; GMBL = Grice Marine Biological Laboratory, College of Charleston, S.C.; LSU = Louisiana State University, Baton Rouge; NCSU = North Carolina State University, Raleigh; NMFS = National Marine Fisheries Service, NOAA (four laboratories—Beaufort, Galveston, Panama City, and La Jolla); OSU = Oregon State University, Corvallis; RSMAS = Rosenstiel School of Marine and Atmospheric Science, University of Miami, Fla.; SCMRRI = South Carolina Marine Resources Research Institute, Charleston; Texas A&M = Texas A&M University, College Station; UNC = University of North Carolina, Institute of Marine Sciences, Morehead City; USNM = U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.; VIMS = Virginia Institute of Marine Science, Gloucester Point.

Specimens

Larval and juvenile specimens used in this study were obtained from several sources. Forty-seven *C. cornutus* specimens from SCMRRI (MARMAP ichthyoplankton survey) collections in the South Atlantic Bight and five specimens from RSMAS collections from the Gulf of Mexico off western Florida were used for morphometrics, counts, and general development. Seven additional RSMAS specimens were used for counts. Other specimens from NMFS (Beaufort) collections in Onslow Bay, off North Carolina, were used for comparison. Twenty-eight *C. gymnorhinus* specimens from SCMRRI collections and 12 from RSMAS collections were used for morphometrics, counts, and general development. Other specimens from NMFS (Beaufort) collections were used for comparison. Fifty-five *C. spilopterus* specimens from NCSU and personal collections in the Cape Fear River estuary, one from a CP&L collection in the ocean just off Cape Fear, and three from Texas A&M collections in the Gulf of Mexico off Texas were used for morphometrics, counts, and general development. Other specimens from Texas A&M, NMFS (Beaufort, Galveston, and Panama City), and RSMAS collections were used for comparison and additional count data. Thirty *E. crossotus* specimens from LSU collections from the Gulf of Mexico off Louisiana and one from a NCSU collection were used for morphometrics, counts, and general development. Other specimens from Texas A&M collections were used for comparison.

Comparative larval material of other species was also examined. *Citharichthys* sp. A (probably *C. abbotti*) specimens came from Texas A&M; *Citharichthys arctifrons* specimens from NMFS (Beaufort), SCMRRI, and VIMS; a *Citharichthys* sp. B (probably *C. dinoceros*) specimen from RSMAS; and *Citharichthys* (*macrops*?) specimens from GCRL, RSMAS, and VIMS. Larvae of the eastern Pacific species *Citharichthys sordidus*, *C. stigmaeus*, and *C. xanthostigma* came from NMFS (La Jolla). Other specimens of Pacific *Citharichthys* spp. came from OSU; *Etropus microstomus* specimens from NMFS (Beaufort) and VIMS; *Etropus* sp. A (probably *E. rimosus*) specimens from CP&L, NMFS (Panama City), and RSMAS; *Cyclopsetta fimbriata* specimens from NMFS (Beaufort), RSMAS, SCMRRI, and Texas A&M; and *Syacium papillosum* specimens from RSMAS and Texas A&M.

Juvenile and adult specimens were examined to determine permanent characters. Specimens of *C. arctifrons*, *C. macrops*, *C. spilopterus*, *E. crossotus*, *E. intermedius* (cf. *E. crossotus*), *E. microstomus*, and *E. rimosus* came from USNM; *Citharichthys cornutus* and *C. gymnorhinus* specimens from GMBL; *Citharichthys macrops* specimens from UNC and a personal collection; and *Citharichthys spilopterus* and *E. crossotus* specimens from NCSU.

Description of caudal skeleton development was based on study of the entire developmental series of *C. cornutus* and comparison with the series of the three other species described. Calcified components of the caudal skeletons of nearly all the specimens could be seen following light staining with Alizarin Red S in 1% aqueous potassium hydroxide solution. Twenty cleared and stained (Taylor 1967) specimens were exam-

ined: *C. arctifrons*, (2) 40, 117 mm SL; *C. cornutus*, (1) 51.5 mm SL; *C. spilopterus*, (2) 41.6, ~100 mm SL; *C. macrops*, (2) 45.7, ~100 mm SL; *E. crossotus*, (1) 49.4 mm SL; *E. microstomus*, (12) ~30-100 mm SL. Radiographs of juveniles and adults also were studied: *C. arctifrons*, (1) 100 mm SL; *C. cornutus*, (16) 30-67 mm SL; *C. gymnorhinus*, (3) 23-37 mm SL; *C. macrops*, (75) 47-113 mm SL; *C. spilopterus*, (65) 23-109 mm SL; *E. crossotus*, (62) 29-92 mm SL; *E. intermedius* (cf. *E. crossotus*), (2) 80, 92 mm SL; *E. microstomus*, (1) 66 mm SL; *E. rimosus*, (1) 104 mm SL.

Counts

All larvae were lightly stained with Alizarin Red S in 1% aqueous potassium hydroxide solution for making counts and observing the sequence of ossification. Most specimens were fairly transparent and internal structures were visible without clearing. The following counts were taken from larvae and juveniles with a stereomicroscope: precaudal neural spines, caudal neural spines, hemal spines, precaudal centra, caudal centra (including urostyle), caudal fin rays supported by each hypural element, dorsal fin rays, anal fin rays, left and right pelvic fin rays, left and right preopercular spines, left and right frontal-sphenotic spines, and left and right upper (premaxillary) and lower (dentary) larval teeth.

Morphometrics

Measurements of various body parts of representative specimens were made on the left side with an ocular micrometer in a stereomicroscope. The only exceptions were standard and total lengths of the six longest *C. spilopterus* (19.4-25.4 mm SL), which were made with dividers and a millimeter scale. Measurements are defined as follows:

Body length (BL) = snout tip to notochord tip for preflexion and flexion larvae (notochord length, NL); snout tip to posterior margin of hypurals for postflexion larvae and juveniles (SL).

Upper jaw length = snout tip to posterior margin of maxillary.

Lower jaw length = anterior tip of dentary to posterior margin of articular just above the angular.

Snout length = horizontal distance from snout tip to anterior margin of left pigmented eye.

Eye diameter = horizontal diameter of left pigmented eye.

Head length (HL) = horizontal distance from snout tip to anterior margin of cleithrum at the body midline.

Snout to anus length = horizontal distance from snout tip through midline of body to vertical line through anus.

Total length = snout tip to posterior margin of finfold prior to caudal fin ray development, then to posterior tip of longest caudal ray.

Head depth = greatest vertical depth of head; in preflexion larvae, this is near or just behind the posterior half of the eye, but with development the greatest depth is progressively more posterior.

Body depth at pelvic fin = vertical distance from dorsal to ventral body margin at base of second pelvic ray.

Body depth at loop of gut = vertical distance from dorsal to ventral body margin at the deepest part of the gut (*C. cornutus* and *C. gymnorhinus* only).

Body depth at anus = vertical distance from dorsal to ventral body margin at anus.

Body depth at third hemal spine = vertical distance from dorsal to ventral body margin at third hemal spine.

Caudal peduncle depth = prior to dorsal and anal fin formation, the vertical distance from dorsal to ventral body margin at the shallowest part of the caudal peduncle; after dorsal and anal fin formation, at the posterior edge of dorsal and anal fins.

Developmental Terminology

Body length is a useful basis for linking characters of unidentified specimens with those in larval descriptions. However, body length may not be the most appropriate basis for comparing larvae of different species, especially bothids, which undergo notochord flexion and transformation at different sizes, usually within a narrow range for a single species but over a wide range for the family or even within a genus (e.g., *Citharichthys*). In this paper, both body length and stage of development are indicated for developmental events. Stage of development is defined by degree of notochord flexion or degree of transformation. Terminology is similar to that of

Moser et al. (1977) and Sumida et al. (1979), with slight modification because of the peculiarities of bothid development.

Preflexion stage = notochord is straight.
Early caudal formation = a substage of preflexion in which the notochord is still straight, but the caudal fin has begun to form.
Flexion stage = notochord is turning upward. There are three substages: Early flexion = notochord is slightly flexed; midflexion = notochord is S-shaped and flexed about 30°-60°; late flexion = notochord is turned up and is no longer S-shaped but is not yet in final position.
Postflexion stage = notochord is in final position, but transformation is not complete.
Transforming larvae = those in which dorsal migration of the right eye can be detected with low magnification. The period of transformation is divided into thirds, depending on the position of the right eye.
Juveniles = those specimens in which the right eye has reached its final position on the left side of the head and in which all fin rays have formed. Reported size ranges at transformation are based on available specimens and might not encompass the full possible size ranges. Environmental stimuli inducing transformation may be encountered at different sizes.

Terminology of components of the caudal skeleton follows Amaoka (1969), except as noted. The caudal fin formula was described by Gutherz (1971) as the number of caudal rays supported by each caudal element, dorsal to ventral.

Gutherz (1971) described certain cranial spines of *Cyclopsetta fimbriata* larvae as originating from the sphenotic bones. Futch and Hoff (1971) described similar spines of *Syacium papillosum* larvae as originating from the frontal bones. In the *Citharichthys* and *Etropus* larvae I have examined, similar spines are at the suture between frontal and sphenotic bones. The origin of these could not be determined with certainty, and therefore they are called "frontal-sphenotic" spines.

For the larvae described here, the first elongate dorsal ray is actually the second ray of that fin.

Larval Identification

Four developmental series were assembled, primarily on the basis of similar meristics, shape, and pigmentation. Transforming larvae and juveniles were identified first by the presence of known adult characters. Additional larval characters observed in those specimens were then used to aid in identification of the smaller specimens.

Because all transformed specimens were sinistral and the right eye of all transforming specimens was migrating, it was decided that the four larval series belonged to one or more of the flatfish families Bothidae, Scophthalmidae, or Cynoglossidae. Morphological characters exhibited in the larval series and shared by larvae of these three families are lateral compression, deep head, deep abdomen, and looped gut, and in early larvae a raised and rounded dorsal profile of the head and slender caudal region. Only one scophthalmid species, *Scophthalmus aquosus*, is known from the western North Atlantic (Gutherz 1967; Hensley 1977). The distinctive rhomboid shape, long-based pelvic fins, and dense pigmentation of *S. aquosus* larvae were lacking in my series of larvae. The small eyes, small head, and confluent dorsal, caudal, and anal fins of cynoglossids were also lacking. In addition, cynoglossids from this region have fewer caudal (usually 9-14) and pelvic (usually 4 left, 0 right) rays than the specimens in my series. Therefore, Scophthalmidae and Cynoglossidae were eliminated from consideration.

Gutherz (1971) summarized known characters most useful for identifying bothid larvae. Futch (1977) summarized subfamilial larval characters and tentatively recognized two subfamilies, Paralichthyinae and Bothinae. The following discussion is limited to western North Atlantic species. Four paralichthyine genera—*Citharichthys*, *Cyclopsetta*, *Etropus*, and *Syacium*—have a similar combination of transitory (larval) and permanent characters that distinguish them from other bothid genera. These include: 1) adult caudal fin ray formula of 4-5-4-4; 2) placement of the left pelvic fin on the ventral midline and the right above the ventral midline, both originating behind the cleithra (Gutherz 1971); 3) the same basic larval shape; 4) similar larval pigmentation—on the gas bladder, in dorsal and anal lines, and in the caudal region; 5) larval preopercular spines (at least in *Citharichthys cornutus*, *C. gymnorhinus*, *C. spilopterus*, *Cyclopsetta fimbriata*, *C. chittendeni*, *Etropus crossotus*, *E. microstomus*, and *Syacium papillosum*); 6) larval frontal-sphenotic spines (at least *Cith-*

arichthys arctifrons, *C. cornutus*, *C. gymnorhinus*, *C. spilopterus*, *Cyclopsetta fimbriata*, *C. chittendeni*, *E. crossotus*, *E. microstomus*, and *S. papillosum*). Caudal formula, pelvic fin placement, shape, and pigmentation of larvae in the four series corresponded to this group.

Cyclopsetta spp. have 26-28 caudal vertebrae (Gutherz 1967). Larvae of *C. fimbriata*, *C. chittendeni*, and *S. papillosum* have 5-10 elongate dorsal rays and well-developed preopercular and frontal-sphenotic spines (Gutherz 1971; Futch and Hoff 1971; Evseenko 1979). Futch and Hoff (1971) listed *Syacium* generic larval characters. Other *Cyclopsetta* and *Syacium* larvae are probably similar. Larvae in the four developmental series had lower caudal vertebral count ranges than *Cyclopsetta* spp., only 2-3 elongate dorsal rays, and relatively small preopercular and frontal-sphenotic spines. Therefore, these two genera were ruled out, leaving *Citharichthys* and *Etropus*. Identification to species is described in the individual species accounts.

For aid in determining species of *Citharichthys* and *Etropus*, frequency distributions of caudal vertebral, anal ray, and dorsal ray counts were tabulated from the literature, and from radiographs of juveniles and adults from the Atlantic off the southeastern United States (Append. Tables 1-3). Ranges of gill raker counts were tabulated from the literature (Append. Table 4). Number of caudal vertebrae (Append. Table 1) was the count most useful for distinguishing larvae. Vertebral counts can be made before ossification during early or midflexion, and overlap is not excessive. However, care is necessary to avoid inaccurate counts because of fused centra. Caudal neural spines and hemal spines, both of which number one less than caudal vertebrae, will stain with alizarin and sometimes can be counted before caudal vertebrae, during early or midflexion. The number of gill rakers on the lower limb of the first arch (Append. Table 4) can be counted in most specimens during transformation and can be very useful for identification of older larvae. The number of anal rays (Append. Table 2) is next in usefulness, followed by the number of dorsal rays (Append. Table 3); however, the overlaps for these counts are great. Efficiency can be gained by plotting individual anal versus dorsal counts on a graph, so that the counts can be used simultaneously. The adult complements of anal and dorsal rays are present by the end of transformation.

After the largest specimens in each series were identified, the identities of successively smaller larvae were verified. The most useful characters for untransformed specimens were lateral, pectoral, and notochordal pigment; number of elongate dorsal rays; number of caudal vertebrae; number and size of left pelvic rays; and head shape.

DESCRIPTION OF DEVELOPMENTAL STAGES

Citharichthys cornutus (Figs. 1-5)

Identification

Larvae approaching transformation had complete complements of countable characters. Those specimens were identified by comparing the following larval counts with known adult counts. Number of specimens is given in parentheses.

Caudal fin formula = 4-5-4-4 (27)
Caudal vertebrae = 25(11)-26(16)
Gill rakers (lower limb, first left) = 12 (1)
Left pelvic rays = 6 (17)
Anal rays = 60-66 (11)
Dorsal rays = 78-84 (11)

Of the potential species listed in Table 1, only *C. cornutus* has counts that agree with these. In addition, larvae were captured over the outer shelf, slightly farther offshore than *C. gymnorhinus* (Fig. 1). This is consistent with bathymetric distribution of adults.

Distinguishing Characters

Citharichthys cornutus larvae have no pectoral melanophore, and notochordal pigment is restricted to the caudal region. Three elongate dorsal rays are present from preflexion (about 4 mm) through transformation. Caudal vertebrae (25-26) can be counted by early flexion (6 mm). Lateral pigment is relatively heavy. Flexion is complete at 9-10 mm SL. The larval mouth and eye are large. Morphology is similar to that of *C. gymnorhinus*. However, the left pelvic fin of *C. cornutus* has a full complement of six rays, and in larvae the first ray is not reduced in size. The left pelvic fin of *C. gymnorhinus* has only five rays, and in larvae the first ray is much reduced compared with that of *C. cornutus*. Length of *C.*

TABLE 1.—Distribution of adults of *Citharichthys* and *Etropus* species known from the western North Atlantic and status of knowledge of their larvae.[1]

Species	Geographic range of adults	Depth range of adults (m)	Larval descriptions
C. arctifrons	Georges Bank to Yucatan	22-682	Richardson and Joseph 1973
E. microstomus	New York to South Carolina	5-91	Richardson and Joseph 1973
C. cornutus	Georgia to Brazil	27-366	This paper
C. gymnorhinus	Florida to Guyana	37-201	This paper
C. spilopterus	New Jersey to Brazil (rare north of Virginia)	1-73	This paper
E. crossotus	Chesapeake Bay to French Guiana	1-86	This paper
C. macrops	Southern Atlantic and Gulf coasts of the United States	1-91	Brief description in Dowd 1978
E. rimosus	North Carolina to Mississippi River	5-190	Brief description in Dowd 1978
C. abbotti	Veracruz to Campeche, Mexico	0-2	Unknown
C. amblybregmatus	Western Caribbean off Nicaragua	139-197	Unknown
C. arenaceus	West Indies to Brazil	Shallow	Unknown
C. dinoceros	Florida to Nicaragua	183-1829	Unknown
C. uhleri[2]	Haiti		Unknown
E. intermedius[3]	Trinidad to Rio de Janeiro	27	Unknown

[1]Distributions compiled from Goode and Bean 1896; Gutherz 1967; Dawson 1969; Gutherz and Blackman 1970; Topp and Hoff 1972; Leslie 1977; Wenner et al. 1979; and original data for *C. spilopterus*, *E. crossotus*, and *C. macrops* (i.e., 1 m depths).
[2]cf. *C. arenaceus*, Dawson 1969.
[3]cf. *E. crossotus*, Gutherz 1967.

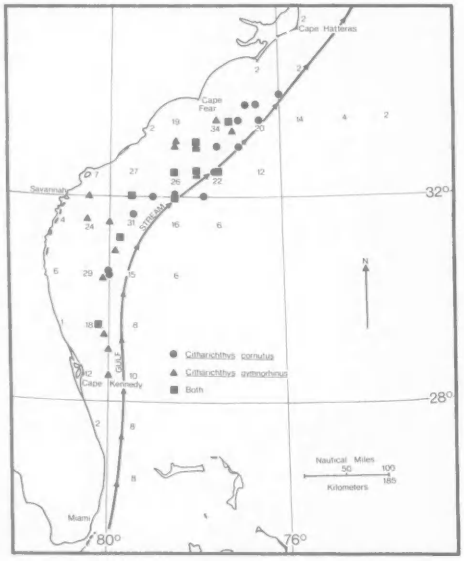


FIGURE 1.—Occurrence of *Citharichthys cornutus* and *C. gymnorhinus* larvae off the southeastern United States. Numbers are the sums of bongo and neuston tows made per 1° quadrangle during four RV *Dolphin* fall, winter, and spring cruises in 1973 and 1974. Symbols indicate positive tows.

cornutus at transformation is about 18 mm. Larvae may appear in collections year-round.

Pigmentation

Pigmentation of *C. cornutus* larvae is relatively heavy. Gas bladder, gut, and lateral tail pigment are the most striking. By 2.2 mm NL and throughout larval development, the dorsal one-third of the left side of the gas bladder is fairly heavily pigmented. This pigment may be diffuse or in the form of stellate or punctate melanophores. With growth, the number of melanophores increases. The maximum number in a preflexion specimen was five (4.8 mm). The right side of the gas bladder is usually unpigmented.

During preflexion (2.2 mm, see Fig. 4A), two or three melanophores are present on both the dorsal and the ventral body margins about halfway between the anus and the notochord tip. Another one or two melanophores are present between these two clusters near the lateral midline. Later in development, pigment in this area forms a band. One or two small melanophores may be present on the ventral finfold just posterior to the hindgut. Three or four melanophores are on the caudal finfold near the ventral body margin just anterior to the notochord tip. Two melanophores are on the ventral surface of the gut loop; additional melanophores appear there during development. A small melanophore appears along the posterodorsal surface of the midgut at about 3 mm. Melanophores begin appearing on the ventral body margin anterior to the cleithrum at about 3 mm. At about 4.7 mm, one or two melanophores appear along the posterior margin of the articular.

Flexion larvae (see Fig. 4B) usually have four or five melanophores on the dorsal one-third of the left side of the gas bladder. Midlateral caudal pigmentation consists of up to six dashlike melanophores. Additional, dashlike clusters of pigment appear along the dorsal and ventral body

margins between the anus and the caudal fin base.

During midflexion (6 mm, see Fig. 4B), internal pigment appears along the dorsal notch between the midbrain and hindbrain, and one or two round melanophores appear below the notch. Visible internal notochordal pigment is restricted to the vicinity of the external caudal band. The dorsal surfaces of one to three forming centra are darkened by about 6 mm. Several melanophores are present along the ventral body margin from just above the tip of the urohyal to just behind the cleithrum. Internal pigment appears between the hindgut and anal fin origin by midflexion.

By late flexion (8 mm, see Fig. 4C), both sides of the gas bladder are obscured by body musculature, and pigment appears diffuse. Notochordal pigment appears as fine dashes along the dorsal surfaces of three to six centra of caudal vertebrae 15-21. As many as 30 or more melanophores may be present along the ventral surface of the gut loop. Pigment along the posterodorsal surface of the midgut extends to the gas bladder and appears as a black lining over the gut. One or more melanophores appear on or just behind the posterodorsal margin of the preopercle. Melanophores have developed along the elongate second left pelvic ray and begin to develop along the elongate dorsal rays at 8-9 mm. Some larvae have small melanophores near the distal tips of rays at the middle of both dorsal and anal fins. By 8 mm, a group of melanophores has appeared along the middle of the caudal fin. The posterior margin of the articular is covered with a stellate melanophore.

By postflexion (9 mm), myoseptal pigment is present in the caudal band as well as adjacent to dorsal and ventral lines. Internal pigment along the brain surface looks diffuse. Pigment appears on the dorsal fin membrane adjacent to the first dorsal ray at about 11 mm. Body musculature tends to obscure dorsal notochordal pigment in larvae longer than 12 mm. Additional midlateral dashlike melanophores appear near the caudal fin base at 13-14 mm (see Fig. 5A). By about 14 mm, all five dorsal and four ventral pigment lines have formed, and myoseptal pigment is well developed. A small amount of pigment is present along the anteroventral edge of the maxillary by about 14 mm. Late transforming larvae have about three small internal melanophores near the pectoral fin base and just forward of the cleithrum beneath the angle of the last gill arch (barely visible through the opercle); these probably develop by about 14 mm. Ventral pigment from the urohyal to the cleithrum persists until late transformation. By late transformation (see Fig. 5B), midlateral dashlike melanophores are present anterior to the caudal band.

Morphology (Figs. 4, 5; Tables 2, 3)

General morphological features include lateral compression, a deep head, a deep abdomen, and a looped gut. In early larvae the dorsal profile of the head is raised and rounded and the caudal region is slender. The eye is nearly spherical during early development but becomes ellipsoidal in transforming larvae. A ventral choroid fissure is visible from 3-4 mm NL until about the end of the postflexion stage. The nasal capsule is visible by about 3 mm NL. The gas bladder is prominent just above the foregut until the end of postflexion. It bulges slightly on the left side of the body and is not as obvious on the right. A loop forms in the gut by 2 mm NL. The liver occupies a large portion of the anteroventral region of the abdomen. Adult morphometrics given in the following discussion were derived from Topp and Hoff (1972).

The mouth is relatively large in larvae and adults. Larval upper jaw length/BL increases slightly from 10.3% (preflexion) to 11.0% (flexion) and then decreases to 9.8% (postflexion). Adult upper jaw length/BL is 12.8%, range 11.8-13.7%. Larval upper law length/HL decreases from 37% to 34%. Adult upper jaw length/HL is 45%. Larval lower jaw length/BL increases slightly from 13.3% (preflexion) to 13.9% (flexion) and then decreases slightly to 13.0% (postflexion). Larval lower jaw length/HL decreases slightly from 48% to 46% and is only slightly greater than that of *C. gymnorhinus*.

Larval snout length is moderate. Larval snout length/BL increases slightly from 6.2% (preflexion) to 7.1% (flexion) and then decreases slightly to 6.3% (postflexion). Adult snout length/BL is 5.5%, range 4.8-6.2%. Larval snout length/HL is constant at about 22-23%. Adult snout length/HL is 19.5%.

The larval eye is large, and the relative size of the adult eye is greater than that of any other western North Atlantic *Citharichthys* or *Etropus* species except *C. amblybregmatus*. Larval eye diameter/BL is constant at 9.8% during preflexion and flexion and then decreases to 8.5% (postflexion). Adult orbit length/BL is 10.0%, range

TABLE 2.—Measurements (mm) of larvae of *Citharichthys cornutus*. Pref = preflexion, ECF = early caudal formation, Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion. S = symmetrical, 1 = 0 to one-third of the way to the dorsal ridge, 2 = one-third to two-thirds of the way to the dorsal ridge, 3 = two-thirds to all the way to the dorsal ridge, R = on the dorsal ridge.

Body length	Upper jaw length	Lower jaw length	Snout length	Eye diameter	Head length	Snout to anus length	Total length	Head depth	Body depth at pelvic fin	Body depth at loop of gut	Body depth at anus	Body depth at third hemal spine	Caudal peduncle depth	Flexion stage	Right eye position
2.2		0.33	0.12	0.27	0.62	1.1		[1]0.76	[1]0.61	[1]0.61	[1]0.53	[1]0.26		Pref	S
3.2	0.35	0.41	0.21	0.31	1.0	1.7		1.2	[1]1.1	[1]1.0	[1]0.79	[1]0.36		Pref	S
3.7	0.40	0.47	0.25	0.37	1.1	1.9	3.8	1.2	[1]1.2	[1]1.2	[1]0.88	[1]0.47		Pref	S
4.0		0.56	0.28	0.44	1.1	1.9		1.4	[1]1.4	[1]1.5	[1]1.2	[1]0.64		Pref	S
4.1		0.59	0.27	0.43	1.2	2.1	4.2		[1]1.3			[1]0.57		Pref	S
4.5	0.47	0.57	0.27	0.43	1.2	1.8	4.6	1.4		[1]1.4	[1]1.1	[1]0.65		Pref	S
4.5	0.44	0.61	0.23	0.40	1.1	1.9	4.6	1.5	[1]1.4	[1]1.5	[1]1.2	[1]0.63		Pref	S
4.6	0.50	0.71	0.29	0.47	1.3	2.2	4.7	1.8	1.7		1.5	0.83		ECF	S
4.8	0.51	0.66	0.26	0.48	1.3	2.2	5.0	1.6	[1]1.6	[1]1.6	[1]1.4	[1]0.82		ECF	S
4.9			0.28	0.47	1.3	2.1	5.0		[1]1.6	[1]1.8	[1]1.5	[1]0.83		ECF	S
5.0	0.58	0.73	0.37	0.53	1.5	2.2		1.7	1.9					ECF	S
5.7	0.48	0.63	0.32	0.50	1.5	2.3	5.8		1.9	1.9	1.9	1.1		ECF	S
5.7	0.53	0.65	0.35	0.52	1.5	2.5		2.0	1.9	2.0		1.0		ECF	S
5.8	0.65	0.81	0.33	0.63	1.7	2.7		2.2	2.5	2.6	2.5	1.6	0.57	Mid	S
6.0	0.63	0.78	0.40	0.53	1.7	2.4		2.1	2.2	2.4	2.2	1.4		Early	S
6.1	0.69	0.86	0.37	0.63	1.8	3.1		2.4	2.7	3.0	2.6	1.8	0.61	Mid	S
6.3	0.66	0.84			1.8	2.6	7.4	2.4	2.5			1.7	0.59	Mid	S
6.3	0.75	0.96	0.46	0.65		3.0		2.5	2.8	3.1	2.7	1.8	0.64	Mid	S
6.4	0.70	0.92	0.41	0.63	1.8	2.9	7.5	2.5	2.8	3.0	2.7	1.8	0.64	Mid	1
6.4	0.70	0.89	0.44	0.63	1.8	3.0	7.2	2.4	2.6	2.8	2.5	1.6	0.54	Mid	S
6.4	0.77	0.90	0.55	0.63		3.0		2.5	2.8	3.1	2.7	1.9	0.65	Late	1
6.9	0.87	1.1	0.53	0.73	2.3	3.2	8.6	2.8	3.2	3.6	3.3	2.3	0.88	Late	1
7.2	0.76	0.96	0.46	0.74	2.2	3.2		2.8	3.0	3.4	3.1	2.1	0.84	Late	S
7.2	0.77	1.0	0.47	0.75	2.2	3.2	8.7	2.7	3.0	3.5	3.3	2.2	0.80	Late	S
7.6	0.90	1.2	0.60	0.77	2.5	3.6		3.2	3.7	4.2	4.0	3.0	1.0	Late	S
7.6	0.77	0.99	0.51	0.73	2.2	3.6	9.2		3.0	3.2	3.0	2.3	0.82	Late	S
7.6	0.83	1.0	0.50	0.77	2.3	3.3		2.8	3.2	3.6	3.3	2.3	0.88	Late	2
7.6	0.84	1.1	0.50		2.3	3.7	9.3	3.0	3.6	4.0	3.5	2.6	0.90	Late	S
7.7	0.90	1.1	0.65	0.73	2.4	3.4		3.2	3.5	3.7	3.5	2.6	0.94	Late	S
7.9	0.81	1.0	0.54	0.74	2.4	3.9	9.5		3.5	3.8	3.6	2.5	0.90	Late	1
8.2	0.91	1.2	0.64	0.81	2.6	3.6			3.7	4.1	4.0	3.0	1.1	Late	1
8.2	0.87	1.1	0.62	0.76	2.5	3.6		3.1	3.4	3.5	3.3	2.5	0.87	Late	1
8.3	0.97	1.3	0.71	0.81	2.7	4.1		3.5	4.0	4.8	4.3	3.0	1.1	Late	1
8.3	0.96	1.2	0.51	0.85	2.6		10.5		4.0	4.6	4.1	3.0	1.1	Late	S
8.4	0.90	1.1	0.61	0.80	2.7	4.2	10.2	3.4	3.8	4.4	3.9	2.8	0.94	Late	1
8.6	0.90	1.1	0.66	0.81	2.7	4.1	10.7	3.2	3.7	4.4	4.1	3.0	1.0	Late	2
8.8	0.95	1.2	0.61	0.80	2.6	3.7		3.2	3.8	3.9	3.9	2.9	1.0	Late	2
8.9	0.90	1.1	0.62	0.80	2.6	3.9		3.4	3.8	4.1	3.8	2.9	1.0	Late	2
10.4	1.1	1.4	0.74	0.93	3.2	4.6	12.9	4.0	4.6	5.3	5.1	4.0	1.4	Post	3
10.6	1.1	1.5	0.77	1.0	3.2	4.8	13.2	4.1	4.8	5.8	5.6	4.1	1.5	Post	3
10.6	1.2	1.5	0.73	0.94	3.2	4.6		3.9	4.6	5.3	5.1	4.1	1.4	Post	1
10.9	1.2	1.5	0.79	0.99	3.2	4.3		4.0	4.7	5.7	5.3	4.1	1.4	Post	3
11.5	1.2	1.6	0.74	1.1	3.4	4.9	14.1	4.0	4.6	5.5	5.3	4.1	1.4	Post	3
12.0	1.1	1.6	0.89	0.99	3.5	4.6	14.7	4.3	4.9	5.1	5.2	4.3	1.4	Post	3
12.1	1.3	1.6	0.73	1.1	3.6	5.0		4.6	5.1	6.1	6.0	4.9	1.6	Post	2
12.8	1.1	1.6	0.64	1.1	3.5	5.0		4.4	4.9	5.8	5.5	4.6	1.6	Post	3
12.9	1.2	1.6	0.73	1.0	3.5	5.1		4.8	5.2	6.1	5.9	4.8	1.6	Post	3
13.0	1.2	1.6	0.72	1.0	3.5	4.8	15.9	4.5	5.4	5.9	5.9	5.3	1.6	Post	3
13.8	1.2	1.7	0.70	1.2	3.7	5.2		5.4	5.9	6.7	6.5	5.5	1.8	Post	3
15.4	1.4	1.8	0.95	1.2	4.0	5.6	18.5	5.1	6.1	6.9	6.8	6.1	1.9	Post	3
17.4	1.6	2.2	1.2	1.2	4.8	5.6	21.2	5.7	6.6	7.5	7.6	7.2	2.2	Post	3
17.4	1.7	2.1	1.0	1.5	4.8	5.6		6.3	6.5		7.7	6.8	2.0	Post	R

[1]Measurement does not include dorsal or anal pterygiophores.

9.2-11.1%. Larval eye diameter/HL decreases from 36% to 30% and is similar to that of *C. gymnorhinus*. Adult orbit length/HL is 35.5%.

The head is relatively large in larvae and moderate in adults. Larval head length/BL increases from 28% (preflexion) to 30% (flexion) and then decreases to 28% (postflexion). Postflexion head length/BL is similar to those of *C. arctifrons* and *C. gymnorhinus*. Adult head length/BL is 28%, range 27-30%. Larval head depth/BL increases from 34% (preflexion) to 39% (flexion) and then decreases slightly to 36% (postflexion).

Larval snout to anus length is relatively great until postflexion. Snout to anus length/BL is 46% during preflexion and flexion and then decreases greatly to 39% (postflexion).

The body is relatively deep in larvae and moderate in adults. Larval body depth at pelvic fin/

TABLE 3.—Body proportions of larvae and juveniles of three species of *Citharichthys* and one species of *Etropus*. Except for body length, values are in percentage of body length (BL) or of head length (HL) and are given as: mean ± standard deviation (range). (Values derived from Tables 2, 5, 6, 7.)

Measurement	*C. cornutus*	*C. gymnorhinus*	*C. spilopterus*	*E. crossotus*
Body length (mm)				
Preflexion	4.6 (3.2-5.7)	4.6 (4.4-5.0)	3.7	4.6
Flexion	7.4 (5.8-8.9)	6.7 (5.3-7.7)	6.4 (5.7-6.8)	6.8 (4.9-9.5)
Postflexion	12.9 (10.4-17.4)	10.4 (7.9-12.9)	9.4 (8.3-10.6)	10.2 (9.3-10.8)
Early juvenile			10.0 (8.7-11.6)	
Midjuvenile			20.5 (14.3-25.4)	
Upper jaw length/BL				
Preflexion	10.3±1.0(8.4-11.6)	9.5±0.7(8.3-10.3)	9.9	7.0
Flexion	11.0±0.6(10.1-12.5)	9.3±0.4(8.3-10.0)	7.2±0.8(6.3-7.9)	7.2±0.7(5.9-8.4)
Postflexion	9.8±0.8(8.6-10.8)	9.3±0.7(8.1-11.3)	6.7±0.6(5.6-7.9)	7.1±0.5(6.4-7.8)
Early juvenile			7.3±0.4(6.1-8.1)	
Midjuvenile			9.0±0.4(8.4-9.7)	
Lower jaw length/BL				
Preflexion	13.3±1.3(11.0-15.3)	11.5±1.0(10.2-12.9)	12.1	9.6
Flexion	13.9±0.9(12.4-15.5)	12.7±0.6(11.6-13.6)	9.9±0.7(9.1-10.4)	9.6±1.0(8.5-12.3)
Postflexion	13.0±0.8(11.9-14.4)	12.7±0.6(11.6-14.2)	9.1±0.5(8.2-10.2)	9.8±0.5(9.2-10.6)
Early juvenile			10.3±0.5(8.9-11.5)	
Midjuvenile			13.1±0.4(12.5-13.8)	
Snout length/BL				
Preflexion	6.2±0.7(5.1-7.4)	5.2±1.1(3.7-6.7)	7.5	5.2
Flexion	7.1±0.8(5.7-8.6)	5.8±0.6(4.9-7.0)	7.6±0.8(6.8-8.1)	6.4±0.7(5.1-7.5)
Postflexion	6.3±0.8(5.0-7.4)	6.1±0.6(4.8-7.6)	6.4±0.6(5.6-7.4)	6.8±0.9(5.4-7.6)
Early juvenile			5.8±0.6(4.4-7.2)	
Midjuvenile			5.0±0.5(4.3-5.5)	
Eye diameter/BL				
Preflexion	9.8±0.7(8.8-11.0)	8.8±0.5(8.1-9.5)	9.7	7.4
Flexion	9.8±0.5(8.8-10.8)	8.9±0.8(6.9-10.0)	7.9±0.2(7.6-8.1)	6.9±0.4(6.1-7.7)
Postflexion	8.5±0.6(7.2-9.4)	8.8±0.5(7.9-9.8)	6.5±0.6(5.5-7.6)	6.3±0.3(6.1-6.9)
Early juvenile			6.8±0.5(5.9-7.7)	
Midjuvenile			7.0±0.6(6.5-8.2)	
Head length/BL				
Preflexion	27.6±2.2(23.8-31.2)	24.8±1.0(23.8-26.6)	28.0	23.4
Flexion	30.4±1.5(28.0-33.1)	27.9±1.9(25.0-31.1)	26.4±0.8(25.5-27.0)	26.4±1.3(24.2-28.7)
Postflexion	28.4±1.6(25.9-30.5)	28.6±1.7(26.8-33.8)	23.9±1.0(22.4-25.7)	26.4±1.5(24.4-28.8)
Early juvenile			25.4±0.8(23.9-27.1)	
Midjuvenile			25.0±0.7(24.2-26.2)	
Snout to anus length/BL				
Preflexion	45.8±4.7(39.4-54.1)	43.0±1.2(42.0-45.1)	40.0	39.1
Flexion	45.9±2.9(40.1-51.2)	44.2±2.0(40.2-46.6)	39.0±1.4(37.5-40.2)	44.2±2.0(39.8-48.0)
Postflexion	39.3±4.1(32.1-45.8)	39.7±2.9(34.6-46.2)	31.8±1.2(29.7-33.5)	38.8±3.2(33.5-42.2)
Early juvenile			31.0±1.3(28.8-34.0)	
Midjuvenile			31.6±1.2(29.8-34.3)	
Total length/BL				
Preflexion	102.3±0.7(101.6-103.5)	102.0±0.6(101.5-102.9)	102.2	101.5
Flexion	121.0±3.9(112.3-126.5)	116.0±12.6(102.0-126.2)	128.0	115.0±8.8(100.7-127.4)
Postflexion	123.0±1.4(120.6-124.9)	121.3±1.0(119.8-122.5)	123.1±1.2(121.4-125.0)	122.3±1.3(119.7-123.4)
Early juvenile			123.9±2.0(119.4-129.4)	
Midjuvenile			125.4±1.6(123.4-128.0)	
Head depth/BL				
Preflexion	34.5±2.3(31.4-38.8)	29.0±1.8(26.7-31.4)	36.6	28.6
Flexion	38.7±2.0(34.3-42.5)	33.3±2.3(28.3-36.2)	39.4±2.0(38.1-41.7)	33.8±1.6(30.7-36.4)
Postflexion	36.2±1.9(32.9-38.8)	33.3±1.6(31.0-36.3)	32.8±1.1(31.0-34.9)	33.1±1.6(31.5-35.8)
Early juvenile			32.0±1.1(29.8-34.9)	
Midjuvenile			31.0±1.0(29.6-33.0)	
Depth at pelvic fin/BL				
Preflexion	33.6±2.0(31.2-37.6)	29.8±2.6(27.0-33.5)	40.3	26.2
Flexion	43.6±2.9(37.1-49.1)	37.5±3.1(31.9-42.7)	46.7±0.9(45.9-47.7)	39.0±4.0(32.7-49.7)
Postflexion	41.3±2.4(37.4-45.8)	39.0±1.7(36.4-43.9)	39.0±1.1(36.9-40.8)	40.2±2.4(36.2-43.6)
Early juvenile			37.2±1.2(34.7-40.3)	
Midjuvenile			35.0±0.9(33.3-36.4)	
Depth at loop of gut/BL				
Preflexion	33.7±1.9(31.0-37.0)	29.2±2.9(25.5-33.9)		
Flexion	48.4±4.4(39.6-57.4)	39.1±4.3(32.7-45.0)		
Postflexion	48.0±3.6(42.6-54.7)	43.9±2.2(41.5-50.2)		
Depth at anus/BL				
Preflexion	28.4±3.6(23.8-33.7)	24.9±2.5(22.4-29.2)	38.7	21.4
Flexion	44.5±4.0(36.1-52.4)	36.9±4.4(30.3-44.2)	50.6±1.2(49.2-51.4)	37.8±5.6(29.3-45.7)
Postflexion	46.6±2.8(43.0-52.9)	42.2±1.7(39.7-47.0)	42.9±1.6(39.9-44.9)	43.1±3.5(36.3-46.2)
Early juvenile			39.5±1.4(35.9-43.3)	
Midjuvenile			38.7±0.7(37.2-39.7)	
Depth at third hemal spine/BL				
Preflexion	15.6±2.5(11.2-19.5)	14.2±2.3(11.9-18.2)	22.6	11.6
Flexion	31.4±3.9(22.8-39.8)	26.6±4.3(19.7-33.2)	40.8±2.9(38.7-44.0)	28.2±7.3(18.2-39.1)
Postflexion	38.6±1.9(35.6-41.8)	34.8±2.8(28.6-42.0)	38.0±1.4(35.3-39.8)	37.7±1.5(36.2-40.2)
Early juvenile			37.0±1.4(34.6-40.0)	
Midjuvenile			40.2±1.0(39.0-42.3)	

TABLE 3.—*Continued.*

Measurement	*C. cornutus*	*C. gymnorhinus*	*C. spilopterus*	*E. crossotus*
Caudal peduncle depth/BL				
Flexion	11.4±1.4(8.4-13.8)	11.6±1.6(9.3-14.4)	14.4±1.6(13.1-16.2)	9.6±3.0(4.7-13.4)
Postflexion	12.7±0.6(11.6-13.8)	13.2±0.7(12.2-14.7)	13.5±0.5(12.7-14.3)	12.6±0.6(11.8-13.4)
Early juvenile			13.6±0.6(12.2-14.6)	
Midjuvenile			11.4±0.6(10.0-12.3)	
Upper jaw length/HL				
Preflexion	37.4±2.7(32.6-40.7)	38.3±2.0(34.9-40.9)	35.6	29.9
Flexion	36.0±1.8(33.2-39.1)	33.3±2.1(29.2-37.6)	27.2±2.4(24.7-29.4)	27.2±2.4(21.6-30.5)
Postflexion	34.4±1.6(31.6-36.6)	32.6±1.9(29.4-37.5)	28.1±2.2(24.0-33.8)	26.9±1.1(24.7-27.6)
Early juvenile			28.7±1.5(25.4-31.3)	
Midjuvenile			36.2±1.4(33.9-38.4)	
Lower jaw length/HL				
Preflexion	48.0±4.9(41.0-56.5)	46.5±3.2(42.7-51.2)	43.3	41.1
Flexion	45.5±2.9(39.5-51.4)	45.6±2.2(42.5-49.6)	37.5±1.4(35.9-38.6)	36.3±3.2(30.8-46.8)
Postflexion	45.9±1.1(43.6-47.7)	44.5±1.8(40.2-46.8)	38.2±1.7(35.9-41.5)	37.2±1.5(35.4-39.0)
Early juvenile			40.5±2.1(36.9-44.1)	
Midjuvenile			52.6±1.5(50.9-55.9)	
Snout length/HL				
Preflexion	22.4±1.5(20.2-25.2)	20.8±4.1(15.4-26.8)	26.9	22.4
Flexion	23.0±2.0(19.3-27.2)	20.9±1.6(19.0-24.6)	28.8±3.3(25.0-31.2)	24.3±1.9(21.0-28.0)
Postflexion	22.3±2.3(18.4-25.5)	21.3±1.9(17.6-24.0)	27.0±2.5(23.2-31.4)	25.9±2.7(22.3-29.1)
Early juvenile			23.0±2.3(18.3-27.1)	
Midjuvenile			19.9±1.7(17.5-22.5)	
Eye diameter/HL				
Preflexion	35.6±2.1(31.0-39.6)	35.4±2.2(32.3-38.2)	34.6	31.8
Flexion	32.2±2.1(29.6-37.5)	31.9±2.7(27.8-39.1)	29.9±0.5(29.4-30.3)	26.0±1.8(22.0-30.6)
Postflexion	29.9±1.5(26.3-31.7)	30.6±1.6(27.4-33.9)	27.1±2.0(23.4-31.1)	23.6±0.4(23.3-24.3)
Early juvenile			26.8±2.0(23.1-30.0)	
Midjuvenile			27.8±1.6(26.4-31.2)	

BL increases from 34% (preflexion) to 44% (flexion) and then decreases slightly to 41% (postflexion). Larval body depth at loop of gut/BL increases from 34% (preflexion) to 48% (flexion and postflexion). Larval body depth at anus/BL increases greatly from 28% to 47%. Larval body depth at third hemal spine/BL increases greatly from 16% to 39%. Adult body depth/BL is 46%, range 43-50%. Larval caudal peduncle depth/BL increases from 11.4% (flexion) to 12.7% (postflexion). Adult caudal peduncle depth/BL is 10.5%, range 9.7-11.4%.

Fin and Axial Skeleton Formation

Development of the caudal skeleton of *C. cornutus* from larva to juvenile (Fig. 2A-E) is typical of the four species described in this paper. The major difference among them is the rate of development. Flexion is complete at about 7-8 mm in *C. gymnorhinus* and *C. spilopterus* and at about 9-10 mm in *C. cornutus* and *E. crossotus*.

During preflexion, before caudal formation (2.2-4.5 mm NL), the notochord is straight and there is no evidence of hypural formation. During early caudal formation (4.6-5.7 mm NL, Fig. 2A) the notochord is straight and the outline of incipient hypurals 2+3 and 4+5 are visible, but neither hypurals nor incipient caudal rays are calcified.

During early flexion (6.0 mm NL, Fig. 2B) the notochord begins to turn upward. Hypurals 2+3 and 4+5 (sometimes hypural 1) and caudal rays begin to stain with alizarin, and the last neural and hemal spines stain with alizarin. Caudal rays form in about equal numbers dorsally and ventrally during flexion, beginning at the posteroventral corner of hypural 4+5 and the posterodorsal corner of hypural 2+3. The 6.0 mm specimen (Fig. 2B) was the smallest in which calcification of caudal rays had begun. During midflexion (6.1-6.4 mm NL, Fig. 2C) the notochord is S-shaped and hypurals 1 and 6 and the epural begin to stain with alizarin. During late flexion (6.4-8.9 mm NL, Fig. 2D) the notochord tip points upward and is nearly flexed but is still in contact with hypural 6 and the epural; all hypurals stain with alizarin and the last neural spine touches hypural 6. All rays are formed by about 7.5 mm NL.

When flexion is complete (10.4-17.4 mm SL, Fig. 2E) the urostyle is separate from hypural 6 and the epural, and all caudal rays stain with alizarin. Fusion of the epural with hypural 6, and fusion of hypural 4+5 with the urostyle occur at about the time of transformation. The terminology of Amaoka (1969) is followed here; however, actual fusion of hypurals 2 with 3 and 4 with 5 was not observed.

The adult caudal skeleton of *C. cornutus* (Fig. 3A) is composed of a urostyle, or terminal half

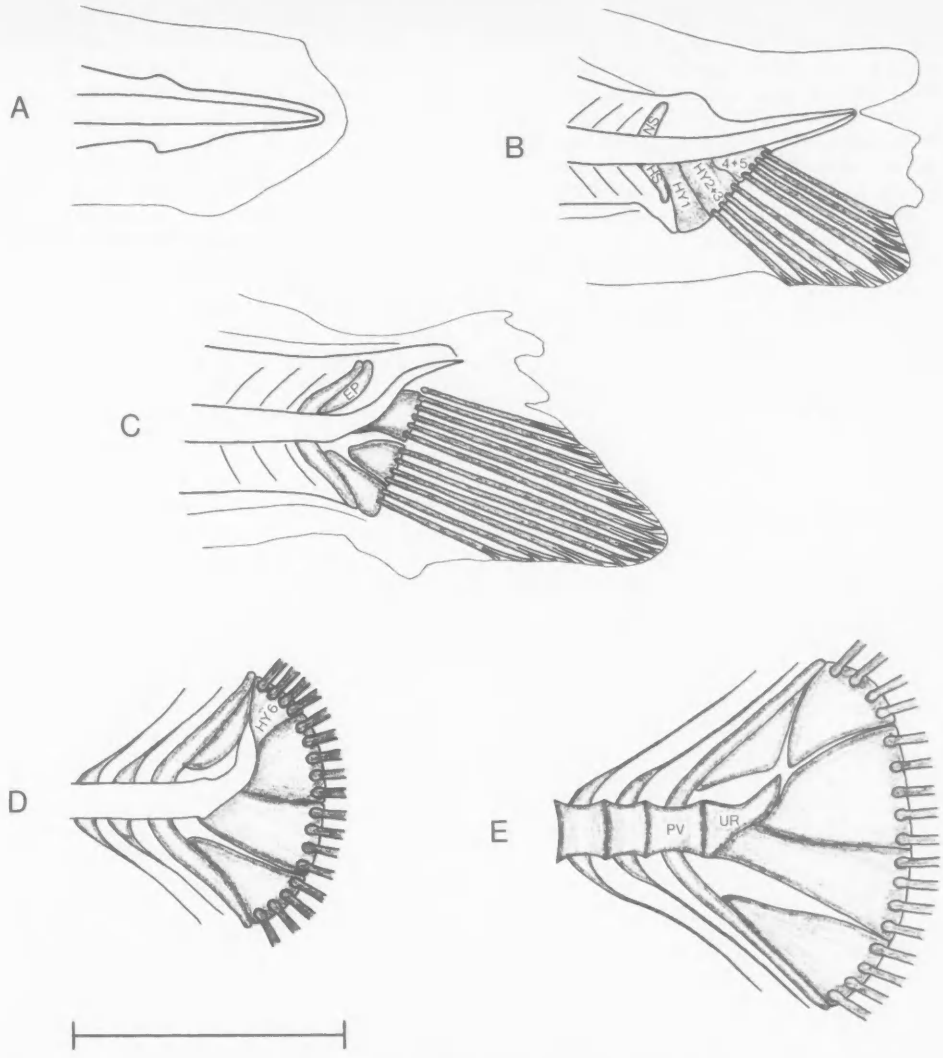


FIGURE 2.—Development of the caudal skeleton of *Citharichthys cornutus*: A. Preflexion (early caudal formation), 5.7 mm NL; B. Early flexion, 6.0 mm NL; C. Midflexion, 6.4 mm NL; D. Late flexion, 8.2 mm NL; E. Postflexion, 13.7 mm SL. NS = neural spine, HS = hemal spine, HY1 = hypural 1, HY2+3 = hypurals 2 and 3, 4+5 = hypurals 4 and 5, HY6 = hypural 6, EP = epural, PV = penultimate centrum, UR = urostyle. Scale = 1 mm.

centrum (according to Hensley 1977, in the bothid *Engyophrys senta* this bone consists of the first and second ural centra and the first preural centrum); a penultimate, or second preural, centrum (see Hensley 1977); an enlarged hemal spine from the second preural centrum supporting hypural 1; autogenous, proximally free, hypural 1 which supports three unbranched and one branched ray (equivalent to "parhypural" of some authors—e.g., Futch 1977; Hensley 1977—

see Sumida et al. 1979); autogenous, fused hypurals 2 and 3, articulating ventrally with the urostyle and supporting four branched rays; fused hypurals 4 and 5, fused with the tip of the urostyle and supporting five branched rays; an autogenous, proximally free element consisting of hypural 6 fused anteriorly with the single epural, one branched and three unbranched rays supported by hypural 6; no evidence of a uroneural; an enlarged neural spine from the second preural centrum supporting the epural. The caudal skeletons of the four species described here are similar to Amaoka's (1969) type 4, except for the lack of a uroneural.

Dendritic splitting of hypurals 2+3 and 4+5 occurs in *Etropus crossotus* by about 40 mm SL (Fig. 3B). The hypurals of adult specimens of *Citharichthys* spp. examined were sometimes grooved but never split as in *E. crossotus*. Hypurals 2+3 and 4+5 of *E. microstomus* and *E. rimosus* were similar to those of *Citharichthys* spp. except for an apparent tendency to split slightly at the distal margins.

In *C. cornutus* larvae all precaudal neural spines stain with alizarin by about 4.8 mm NL. Some caudal neural spines and hemal spines stain with alizarin at 4.8 mm NL and all do by 6.1 mm NL. The urostyle stains with alizarin at 6.3 mm NL. All precaudal and caudal centra stain with alizarin by 7.2 mm NL. The smallest speci-

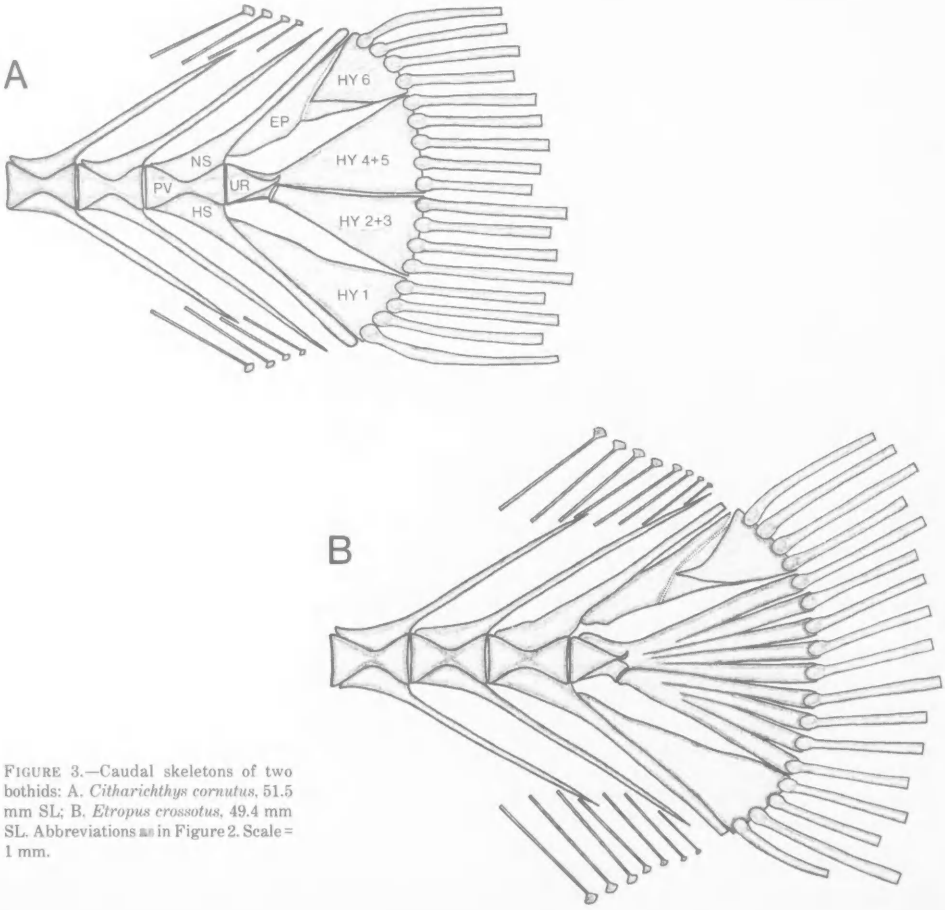


FIGURE 3.—Caudal skeletons of two bothids: A. *Citharichthys cornutus*, 51.5 mm SL; B. *Etropus crossotus*, 49.4 mm SL. Abbreviations as in Figure 2. Scale = 1 mm.

men in which caudal centra could be counted was 5.8 mm NL (midflexion).

The second, third, and fourth dorsal rays are elongate and widely separated at the bases from preflexion (about 4 mm NL) through transformation (17.4 mm SL). During early caudal formation (5.0 mm NL), rays near the middle of the dorsal fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (6.4 mm NL) onward. The first ray and the most posterior rays are calcified just prior to transformation (17.4 mm SL).

During early caudal formation (5.0 mm NL), anal rays near the middle of the fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (about 8 mm NL) onward. The most posterior rays are calcified just prior to transformation (17.4 mm SL).

Development of the left pelvic fin precedes that of the right fin. The left pelvic fin bud appears during preflexion (3.7 mm NL). Rays develop between preflexion (4.0 mm NL) and late flexion (about 8.9 mm NL). The most anterior two rays are the first to appear; the second is elongate and the first slightly elongate. The right pelvic fin bud appears during early caudal formation (4.9 mm NL). Rays develop between midflexion (6.0 mm NL) and late or postflexion (9-10 mm BL). Each complete fin has six rays.

Rayless, fanlike, larval pectoral fins were present on the smallest available specimen (preflexion, 2.2 mm NL). Calcification of rays in the left fin occurs between about 13 mm and 17.4 mm SL. Calcification of rays in the right fin had not begun in the largest specimen (17.4 mm SL).

Cephalic Spination

Preopercular spines (Table 4) were present in the smallest preflexion specimen (2.2 mm NL, Fig. 4A). With development (Fig. 4B, C), additional spines appear until maximum numbers of about 33 on the left (range 26-52) and 39 on the right (range 23-50) are reached during late flexion (6.4-8.9 mm NL). Thereafter, spines are lost until none or only a few remain at transformation (17.4 mm SL, Fig. 5B).

Frontal-sphenotic spines were evident in the second smallest preflexion specimen (3.2 mm NL) and throughout the larval series, though less conspicuous near transformation (13-17 mm SL). The lowermost spine on the left side is usually just above the center of the eye and on the right side slightly anterior to the center of the eye. (During transformation those on the right side are at the anterior margin of the skull.) The spines are arranged in a slightly posteriorly concave arch following the curve of the skull. There are usually six (up to eight) spines per side, including three stronger spines arising from a small bulge of the skull.

Larval Teeth (Table 5)

No teeth are present at 2.2 mm NL (Fig. 4A). At 3.2-4.1 mm NL, larvae usually have two upper and two lower teeth on each side. A 5.3 mm NL preflexion specimen had three upper and four lower teeth on each side. The same numbers were present in the largest early caudal formation specimen (5.7 mm NL). During flexion, numbers of teeth increase from about four upper and five lower (about 6 mm NL) to about eight upper and seven lower (8.9 mm NL) on each side. Postflexion larvae (10.4-13.8 mm SL) have about nine upper and nine lower teeth on each side. The nearly transformed specimen (17.4 mm SL, Fig. 5B) had fewer upper teeth on the left side (about 11) than on the right side (19) but the same number (about 15) in both lower jaws.

Transformation

Migration of the right eye may begin as early as midflexion (6.4 mm NL) or as late as postflexion (10.6 mm SL). The right eye moves from the right side of the head through a space between the dorsal fin and supraorbital bars (Fig. 5A) as in *Cyclopsetta fimbriata* (Gutherz 1971). The right eye reaches its final position on the left side of the head by about 18 mm SL. No early juvenile specimen was available, but eye migration in one of the 17.4 mm specimens was nearly complete (Fig. 5B).

Occurrence

Larvae were collected in the Atlantic during February, March, April, May, October, and November (Powles[4]). There was no apparent size progression by month, indicating an extended spawning season. Water depth was 46-640 m.

[4]H. W. Powles, Assistant Marine Scientist, South Carolina Marine Resources Research Institute, P.O. Box 12559, Charleston, SC 29412, pers. commun. July 1976.

TABLE 4.—Number of left and right preopercular spines by stage of larval development. Pref = preflexion, ECF = early caudal formation (preflexion), Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion, Trans = right eye on or past dorsal ridge.

Species	Stage	BL range (mm)	Left			Right		
			$\bar{X}$	N	Range	$\bar{X}$	N	Range
Citharichthys cornutus	Pref	2.2- 5.0	12.1	7	4-18	12.7	7	4-19
	ECF	4.7- 5.7	18.2	4	13-20	19.8	4	18-23
	Early	6.0	23	1		22	1	
	Mid	5.6- 6.4	26.4	7	21-30	31.1	7	26-34
	Late	6.4- 8.9	32.9	19	26-52	38.7	19	23-50
	Post	10.4-13.8	22.0	8	11-33	33.8	8	24-44
	Trans	17.4	~0	1		~4	1	
Citharichthys spilopterus	ECF	3.7	31	1		27	1	
	Late	5.7- 6.7	31	2	26-36	35.5	2	33-38
	Post	8.3-10.2	16.0	7	2-29	20.0	6	11-32
	Trans	8.7-10.2	17.4	5	0-41	21.5	4	1-44
Citharichthys gymnorhinus	Pref	4.5- 5.4	15.3	3	13-17	17.0	3	16-19
	ECF	4.6- 5.3	20.0	2	19-21	14.0	2	11-17
	Early	5.3- 6.0	21.7	3	17-27	24.3	3	21-28
	Mid	6.6	21.0	2	19-23	27.0	2	26-28
	Late	6.7- 7.5	23.0	6	17-29	26.8	6	20-35
	Post	8.3-10.2	31.4	5	25-38	38.6	5	34-43
Etropus crossotus	ECF	4.6	17	1		19	1	
	Early	4.9- 5.4	19.0	2	17-21	21.5	2	21-22
	Mid	5.4- 6.0	24.5	10	18-29	22.0	10	16-27
	Late	6.1- 9.5	15.9	12	7-20	15.2	12	10-20
	Post	9.3-10.8	10.6	5	4-18	8.6	5	3-13
	Trans	10.3	0	1		2	1	

TABLE 5.—Number of larval teeth by developmental stage. Pref = preflexion, ECF = early caudal formation (preflexion), Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion, Trans = right eye on or past dorsal ridge, UJ = upper jaw, LJ = lower jaw.

Species	Stage and BL range (mm)	Jaw	Left			Right		
			$\bar{X}$	N	Range	$\bar{X}$	N	Range
Citharichthys cornutus	Pref	UJ	1.9	8	0- 3	1.9	8	0- 3
	2.2- 5.3	LJ	2.4	8	0- 4	2.4	7	0- 4
	ECF	UJ	3	3	3	3	5	3
	4.7- 5.7	LJ	3.5	4	3- 4	3.5	4	3- 4
	Early	UJ	4	1		4	1	
	6.0	LJ						
	Mid	UJ	5.8	4	5- 6	5.5	6	5- 6
	6.1- 6.4	LJ	6.5	4	6- 7	6.0	5	5- 7
	Late	UJ	6.6	20	5- 8	6.8	17	5- 8
	6.4- 8.9	LJ	6.8	13	6- 8	6.9	13	6- 8
	Post	UJ	8.6	10	8-10	8.9	8	8-10
	10.4-13.8	LJ	8.7	7	8-11	8.7	7	8-10
	Trans	UJ	~11	1		19	1	
	17.4	LJ	~15	1		~15	1	
Citharichthys spilopterus	ECF		2	1		2	1	
	3.7		3	1		3	1	
	Late	UJ	4	3	3- 5	4.3	3	4- 5
	5.7- 6.8	LJ	5	1		4.5	2	4- 5
	Post	UJ	4.0	6	3- 5	3.8	5	3- 4
	9.0-10.6	LJ	4.8	4	4- 5	5	1	
	Trans	UJ	4.8	5	4- 6	4	1	
	9.1-10.7	LJ	5.3	3	5- 6			
Citharichthys gymnorhinus	Pref	UJ	2.3	3	2- 3	2.3	3	2-3
	4.5- 5.4	LJ	2.7	3	2- 4	2.7	3	2-4
	ECF	UJ	2.5	2	2- 3	2.5	2	2-3
	4.6- 5.3	LJ	3.5	2	3- 4	3.5	2	3-4
	Early	UJ	3.3	3	2- 4	3.3	3	2-4
	5.3- 6.0	LJ	4.5	2	4- 5	4.5	2	4-5
	Mid	UJ	4.7	3	4- 5	4.5	2	4-5
	6.4- 6.6	LJ	5.5	2	5- 6	6	1	
	Late	UJ	5.7	6	4- 7	5.3	6	4-7
	6.7- 7.7	LJ	6.5	4	6- 8	6.5	4	6-8
	Post	UJ	7.1	11	6- 8	6.9	9	6-8
	7.9-12.9	LJ	8.0	7	6- 9	8.0	5	8
Etropus crossotus	ECF	UJ	3	1		3	1	
	4.6	LJ	5	1		5	1	
	Early	UJ	3	2	3	3	2	3
	4.9- 5.4	LJ	5.5	2	5- 6	5.5	2	5-6
	Mid	UJ	3.4	10	3- 5	3.4	10	3-5
	5.4- 6.0	LJ	6.4	8	5- 7	6.7	9	5-7
	Late	UJ	4.1	11	3- 5	3.8	9	3-4
	6.1- 9.5	LJ	7.0	10	6- 8	7	7	7
	Post	UJ	4.5	4	4- 5	5.2	5	4-7
	9.3-10.8	LJ	7.2	4	5-10	7.4	5	6-9
	Trans	UJ	7	1		7	1	
	10.3	LJ	>9	1		>9	1	

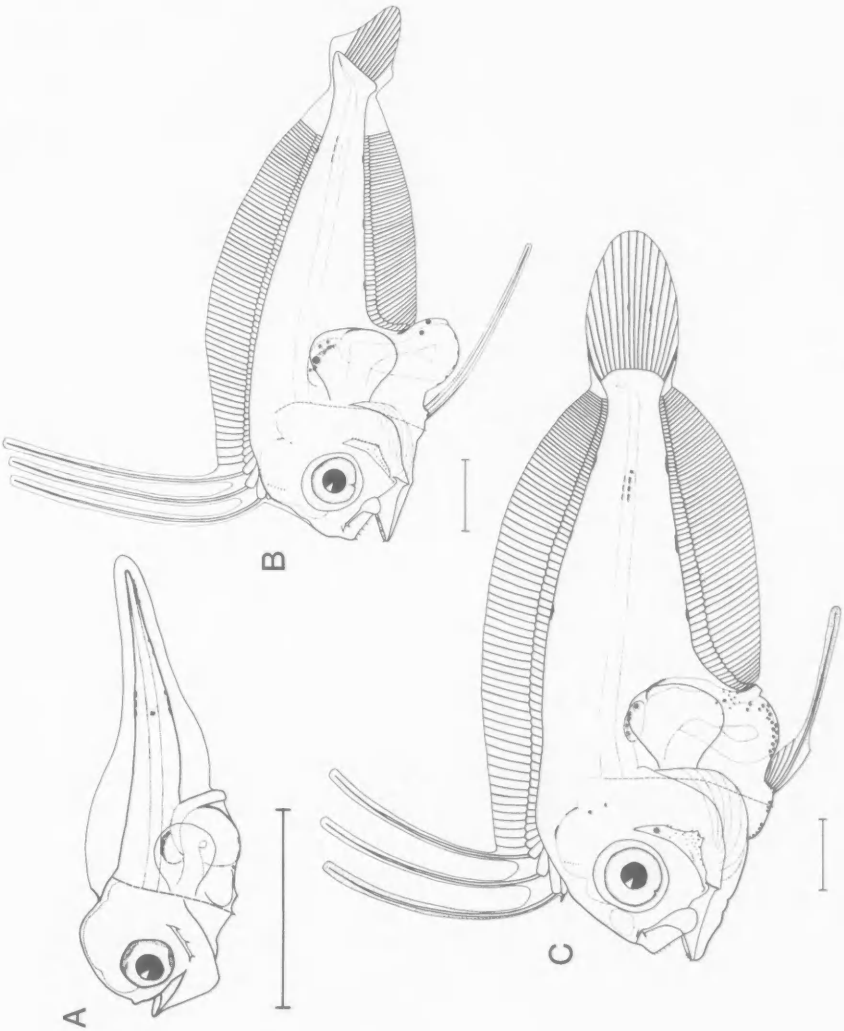


FIGURE 4.—Larval stages of *Citharichthys cornutus*: A. Preflexion, 2.2 mm; B. Midflexion, 6.9 mm; C. Late flexion, 8.2 mm. Scale = 1 mm.

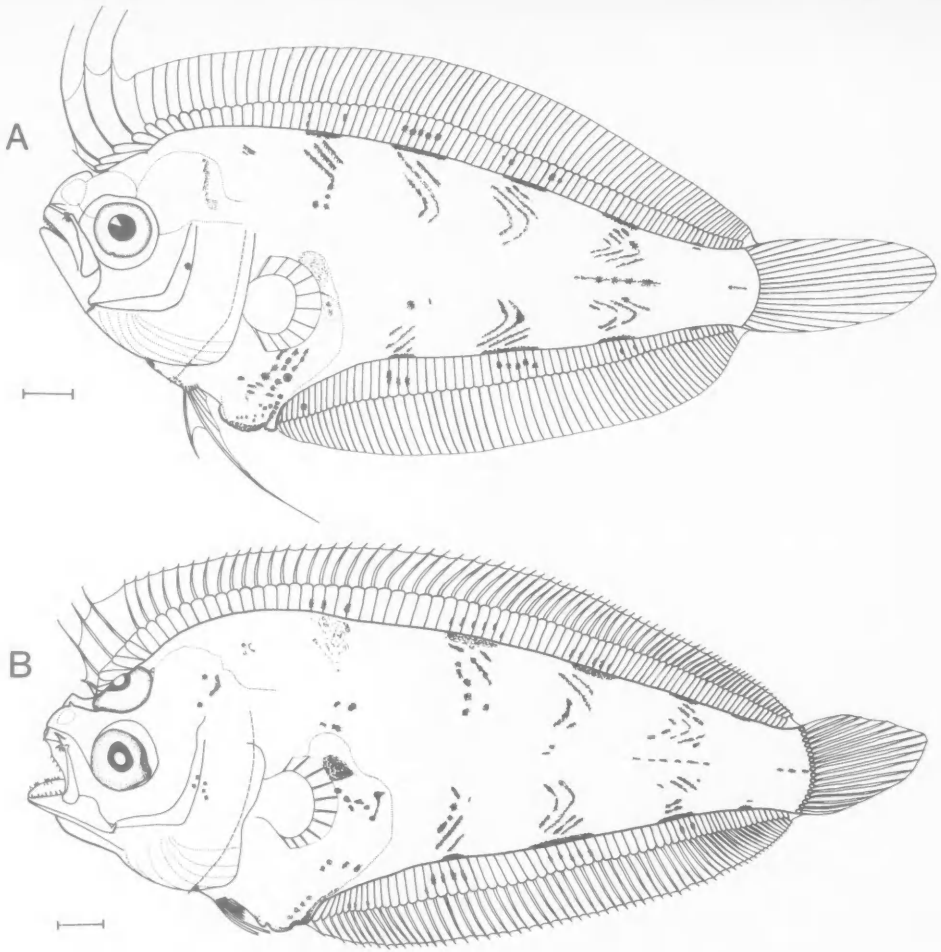


FIGURE 5.—*Citharichthys cornutus*: A. Transforming larva, 14.2 mm; B. Nearly transformed larva, 17.4 mm; C. Adult, 37.2 mm. Scale = 1 mm.

Surface temperature and salinity were 20.4°-27.3°C and 35.5-36.8 ‰. Almost no larvae were caught east of the average Gulf Stream axis (Fig. 1). The reported northern limit for adults is Florida (with one exception— an adult male taken off Cape Hatteras (Stewart[5])). Larval occurrences shown in Figure 1 are evidence of the effectiveness of Gulf Stream transport. The eastward shift of positive tows just north of lat. 32°N corresponds to the location of a semipermanent meander of the Gulf Stream induced by the Charleston Rise (at about lat. 32°N, long. 79°W (Pietrafesa et al. 1978)).

In the eastern Gulf of Mexico, larvae smaller than 4 mm NL were common in January, February, May, June, July, August, and November, indicating year-round spawning in that area (Dowd 1978).

[5]D. J. Stewart, Graduate Student, Laboratory of Limnology, University of Wisconsin, Madison, WI 53706, pers. commun. June 1978.

Citharichthys gymnorhinus (Figs. 1, 6, 7)

Identification

Larvae approaching transformation had complete complements of countable characters. Those specimens were identified by comparing the following larval counts with known adult counts. Number of specimens is given in parentheses.

Caudal fin formula = 4-5-4-4 (15)
Caudal vertebrae = 23(3)-24(18)
Gill rakers (lower limb, first left) = ~12 (1)
Left pelvic rays = 5 (12)
Anal rays = 55-59 (11)
Dorsal rays = 70-75 (11)

Of the potential species listed in Table 1, only *C. gymnorhinus* has counts that agree with these (it is unique in having only five left pelvic rays). In addition, larvae were captured over the outer shelf, but not as far offshore as *C. cornutus* (Fig. 1). This is consistent with bathymetric distribution of adults.

Distinguishing Characters

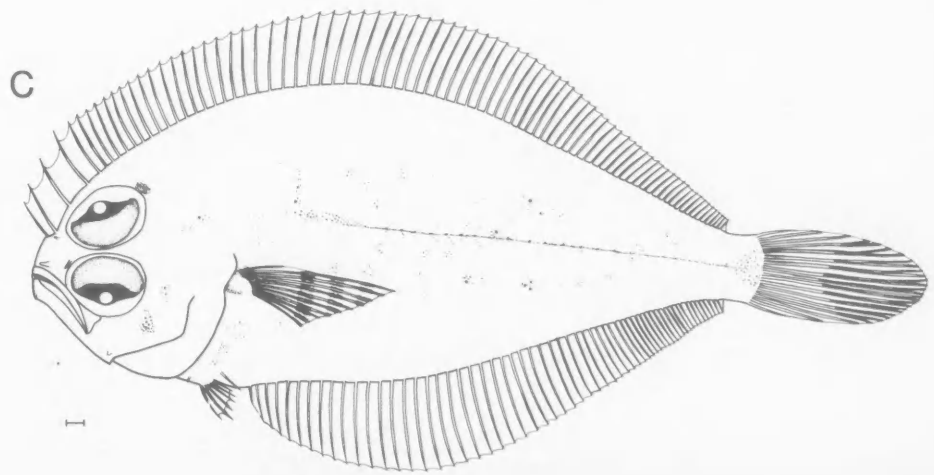
Citharichthys gymnorhinus larvae have no pectoral melanophore, and notochordal pigment is restricted to the caudal region. Three elongate dorsal rays are present from preflexion (4.6 mm) through postflexion (probably through transformation). Caudal vertebrae (23-24) can be counted by early flexion (6 mm). Lateral pigment is relatively sparse except for the caudal band. Flexion is complete at 7-8 mm SL. Morphology is similar to that of *C. cornutus*. However, the left pelvic fin of *C. gymnorhinus* has a full complement of only five rays, and in larvae the first ray is much reduced in size compared with that of *C. cornutus*. Length of *C. gymnorhinus* at transformation is probably about 18 mm. Larvae may appear in collections year-round.

Pigmentation

Pigmentation of *C. gymnorhinus* larvae is moderate. Gas bladder and caudal band pigment are the most striking.

By 4.6 mm and throughout larval development, the dorsal one-third of the left side of the gas bladder is fairly heavily pigmented, usually with distinct melanophores. With growth, the number of melanophores increases. There are usually more of them than in *C. cornutus* larvae. The maximum number in a preflexion specimen was about 15 (4.6 mm, Fig. 6A). The right side of the gas bladder is either unpigmented or has only one or two melanophores.

By 4.6 mm (Fig. 6A) a caudal band of melanophores is present on the dorsal and ventral finfolds and sides and margins of the body about halfway from the anus to the notochord tip. This band is more distinct and regular than in other



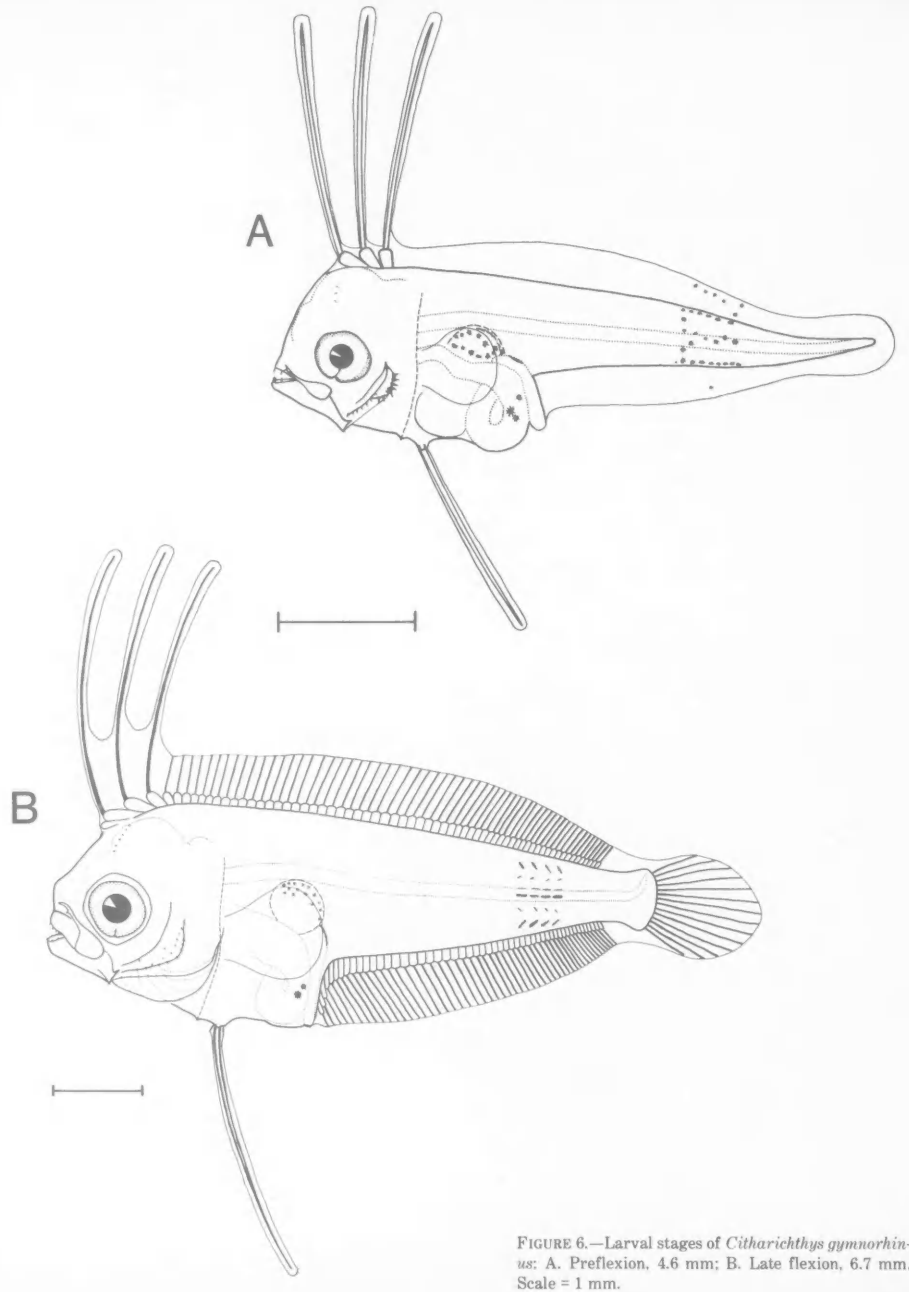


FIGURE 6.—Larval stages of *Citharichthys gymnorhinus*: A. Preflexion, 4.6 mm; B. Late flexion, 6.7 mm. Scale = 1 mm.

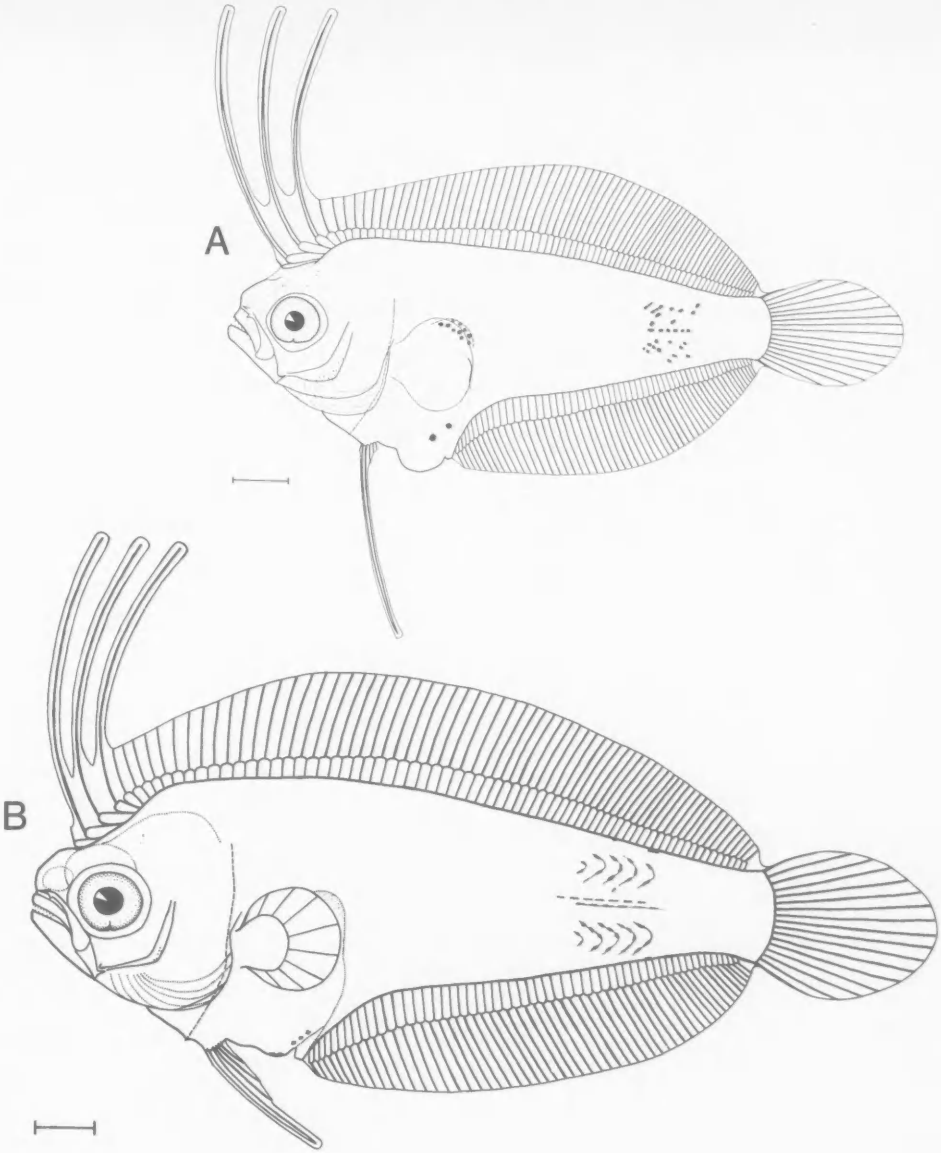


FIGURE 7.—Larval stages of *Citharichthys gymnorhinus*: A. Transforming, 9.6 mm; B. Transforming, 12.6 mm. Scale = 1 mm.

known larvae of western North Atlantic *Citharichthys* and *Etropus* species. In preflexion larvae, before pelvic rays form, one or two melanophores are present on the ventral body margin at the future site of the pelvic fin. By 4.6 mm and throughout development (at least to 13 mm), a few external melanophores are present along the posterior surface of the gut loop. A small melanophore is found over the posterodorsal surface of the midgut of preflexion larvae.

Flexion larvae (Fig. 6B) usually have 15-20 melanophores on the dorsal one-third of the left side of the gas bladder. The caudal band is mostly confined to the body and contains myoseptal pigment. Visible internal notochordal pigment is restricted to the vicinity of the external caudal band. The dorsal surfaces of one or two forming centra are darkened at about 5 mm. By about 6 mm and throughout development (at least to 13 mm), there may be a few melanophores along the ventral surface of the gut loop. By late flexion, notochordal pigment appears as fine dashes along four to six centra of caudal vertebrae 13-19. By late flexion, pigment along the posterodorsal surface of the midgut extends to the gas bladder and appears as a black lining over the gut.

By postflexion (about 8 mm, Fig. 7A), both sides of the gas bladder usually are obscured by body musculature, and pigment in this area appears diffuse. Small melanophores appear on the left pelvic fin membrane along both sides of the elongate second ray. Body musculature tends to obscure notochordal pigment in larvae longer than 12 mm.

Morphology (Figs. 6, 7; Tables 3, 6)

General morphological features are similar to those of *C. cornutus*, with the qualification that the smallest *C. gymnorhinus* specimen examined was 4.6 mm NL. Adult morphometrics given in the following discussion were derived from Gutherz and Blackman (1970) and Topp and Hoff (1972).

The mouth is relatively large in larvae and adults. Larval upper jaw length/BL is fairly constant at 9.3-9.5%. Adult upper jaw length/BL is 11.2%, range 9.9-13.0%. Larval upper jaw length/HL decreases greatly from 38% (preflexion) to 33% (flexion and postflexion). Adult upper jaw length/HL is 41%, range 39-45%. Larval lower jaw length/BL increases from 11.5% to 12.7%. Adult lower jaw length/BL is 13.2%, range 11.6-14.8%. Larval lower jaw length/HL decreases slightly from 46% to 44% and is only slightly less than that of *C. cornutus*. Adult lower jaw length/HL is 48%, range 43-53%.

The larval snout is pointed but relatively short. Larval snout length/BL increases slightly from 5.2% to 6.1%. Adult snout length/BL is 5.4%, range 4.6-6.6%. Larval snout length/HL is constant at 21%. Adult snout length/HL is 20%, range about 18-20%.

The eye is relatively large in larvae and adults (only slightly smaller than that of *C. cornutus*). Larval eye diameter/BL is constant at about 8.8%. Adult orbit length/BL is 9.6%, range 8.0-11.4% (Topp and Hoff 1972); eye diameter/BL is 10.1%, range 9.1-11.0% (Gutherz and Blackman 1970). Larval eye diameter/HL decreases from 35% to 31% and is similar to that of *C. cornutus*. Adult orbit length/HL is 35% (Topp and Hoff 1972); eye diameter/HL is 36.5%, range 33-38% (Gutherz and Blackman 1970).

The head is fairly long but shallow in larvae and of moderate length in adults. Larval head length/BL increases greatly from 25% to 29%. Postflexion head length/BL is similar to those of *C. arctifrons* and *C. cornutus*. Adult head length/BL is 27%, range 25-29%. Larval head depth/BL increases from 29% to 33% and is similar to that of *E. crossotus*.

Larval snout to anus length is fairly great until postflexion. Snout to anus length/BL increases slightly from 43% (preflexion) to 44% (flexion) and then decreases to 40% (postflexion). This length is similar to that of *E. crossotus* during flexion and postflexion.

With the exception of a relatively deep caudal peduncle, the body is of moderate depth in larvae and adults. Larval body depth at pelvic fin/BL increases from 30% to 39%. Larval body depth at loop of gut/BL increases from 29% to 44%. Larval body depth at anus/BL increases greatly from 25% to 42% and during flexion and postflexion is similar to that of *E. crossotus*. Larval body depth at third hemal spine/BL increases greatly from 14% to 35%. Adult body depth/BL is 47%, range 39-50%. Larval caudal peduncle depth/BL increases from 11.6% (flexion) to 13.2% (postflexion). Adult caudal peduncle depth/BL is 11.5%, range 10.5-12.6%.

Fin and Axial Skeleton Formation

Caudal skeleton development is similar to that of *C. cornutus*. Size ranges of available speci-

TABLE 6.—Measurements (mm) of larvae of *Citharichthys gymnorhinus*. Pref = preflexion, ECF = early caudal formation, Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion. S = symmetrical, 1 = 0 to one-third of the way to the dorsal ridge, 2 = one-third to two-thirds of the way to the dorsal ridge, 3 = two-thirds to all the way to the dorsal ridge.

Body length	Upper jaw length	Lower jaw length	Snout length	Eye diameter	Head length	Snout to anus length	Total length	Head depth	Body depth at pelvic fin	Body depth at loop of gut	Body depth at anus	Body depth at third hemal spine	Caudal peduncle depth	Flexion stage	Right eye position
4.4	0.45	0.53	0.24	0.42	1.2	1.9	4.6	1.2	[1]1.4	[1]1.4	[1]1.2	[1]0.69		ECF	S
4.5	0.41	0.49			1.1	2.0				[1]1.3	[1]1.0	[1]0.53		Pref	S
4.6	0.38	0.50	0.21	0.40	1.1	2.1	4.6	1.4	[1]1.3	[1]1.3	[1]1.1	[1]0.60		ECF	S
4.6	0.44	0.56	0.25	0.39	1.1	2.0		1.2	[1]1.3	[1]1.3	[1]1.1	[1]0.64		Pref	S
4.6	0.43	0.47	0.17	0.42	1.1	2.0	4.7	1.4	[1]1.2	[1]1.2	[1]1.1	[1]0.59		Pref	S
5.0	0.52	0.65	0.34	0.41	1.3	2.1	5.1	1.5	1.7	1.7	1.5	0.92		ECF	S
5.3	0.50	0.66	0.26	0.52	1.3	2.4		1.7	1.8	1.9	1.6	1.1		Early	S
5.9	0.55	0.73	0.31	0.51	1.5	2.4		1.7	1.9	1.9	1.8	1.2		Early	S
6.0	0.50	0.70	0.30	0.42	1.5	2.5	6.2	1.7	2.0	2.0	2.0	1.2		Early	S
6.4	0.59	0.86	0.43	0.54	1.8	2.9		2.2	2.4	2.7	2.3	1.6	0.67	Mid	S
6.6	0.61	0.85	0.36	0.63	1.9	3.0		2.3	2.5	2.8	2.5	1.9		Mid	S
6.6	0.60	0.79	0.37	0.58	1.8	2.9		2.1	2.3	2.3	2.2	1.6	0.64	Mid	2
6.7	0.63	0.84	0.40	0.59	1.9	2.8		2.3	2.5	2.4	2.4	1.8	0.70	Late	S
6.8	0.63	0.83	0.41	0.60	1.8	2.9		2.3	2.6	2.8	2.6	1.8	0.76	Late	2
6.7	0.65	0.90	0.38	0.60	1.9	3.2			2.7	3.0	2.7	2.0	0.82	Late	1
6.9	0.63	0.83	0.38	0.59	1.9	3.2		2.2	2.5	2.5	2.3	1.6	0.64	Late	2
7.2	0.67	0.98	0.44	0.72	2.2	3.1	8.6	2.5	2.9		3.0	2.3	0.94	Late	1
7.2	0.69	0.94	0.40	0.63	2.1	3.3		2.6	2.9	3.0	2.9	2.1	0.90	Late	1
7.2	0.72	0.96	0.51	0.62	2.1	3.2		2.4	2.7	2.8	2.7	2.0	0.84	Late	1
7.5	0.68	0.99	0.49	0.67	2.3	3.5		2.7	3.1	3.4	3.3	2.5	1.0	Late	2
7.7	0.72	0.99	0.48	0.77	2.3	3.5	9.7	2.8	3.3	3.4	3.2	2.5	1.1	Late	2
7.9	0.79	1.1	0.50	0.73	2.7	3.4		2.8	3.3	3.6	3.4	2.6	1.0	Post	1
8.2	0.93	1.2	0.63	0.81	2.6	3.8	9.9	3.0	3.6	4.1	3.9	2.9	1.2	Post	3
8.3	0.75	1.0	0.47	0.74	2.3	3.4		2.9	3.2	3.4	3.3	2.4		Post	2
8.6	0.80	1.1	0.47	0.78	2.4	3.6	10.4	3.0	3.4	3.6	3.5	2.7	1.1	Post	2
9.0	0.83	1.2	0.52	0.77	2.6	3.7		3.2	3.6		3.9	3.2	1.3	Post	3
9.6	0.94	1.3	0.64	0.87	2.8	3.9	11.6	3.2	3.8	4.3	4.1	3.4	1.3	Post	2
9.8	0.91	1.3	0.63	0.84	2.8	4.1		3.2	3.8	4.3	4.2	3.4		Post	2
9.8	0.92	1.2	0.60	0.87	2.8			3.1	3.8			3.3	1.2	Post	3
9.9	0.85	1.2	0.60	0.84	2.8	4.0	12.0	3.3	3.7	4.2	4.0	3.1	1.3	Post	2
10.2	0.94	1.2	0.63	0.92	2.8	4.2	12.5	3.5	4.0	4.5	4.4	3.5	1.3	Post	3
10.4	0.93	1.3	0.50	0.95	2.8	4.2		3.6	3.9	4.4	4.3	3.5	1.4	Post	3
10.6	0.98	1.4	0.71	0.87	3.1	4.0			4.2	4.6	4.5	3.9	1.5	Post	2
11.2	1.0	1.4	0.54		3.1	4.2		3.6	4.4	4.9	4.8	4.0	1.5	Post	2
11.7	1.2	1.4	0.74	0.99	3.2	4.5		3.7	4.5	5.0	4.9	4.0	1.5	Post	3
11.7	0.95	1.5	0.70	0.92	3.2	4.0		3.7	4.4	5.2	4.9	4.4	1.4	Post	3
12.6	1.1	1.6	0.73	1.1	3.5	4.6	15.3	4.0	4.9		5.2	5.3	1.7	Post	3
12.9	1.2	1.7	0.84	1.2	3.6	4.8		4.2	5.0	5.7	5.5	4.8	1.6	Post	3
12.9	1.2	1.6	0.78	1.1	3.7	4.5		4.0	4.8	5.4	5.2	4.7	1.7	Post	3
12.9	1.1	1.5	0.82	1.0	3.6	5.0	15.8	4.1	4.7	5.8	5.5	4.4	1.7	Post	2

[1]Measurement does not include dorsal or anal pterygiophores.

mens in each stage are as follows: Preflexion, 4.5-5.4 mm NL; early caudal formation, 4.4-5.3 mm NL; early flexion, 5.3-6.0 mm NL; midflexion, 6.0-6.6 mm NL; late flexion, 6.7-7.7 mm NL; postflexion, 7.9-12.9 mm SL. Caudal rays become calcified between early flexion (5.9 mm NL) and late flexion (7.2 mm NL).

All precaudal neural spines stain with alizarin by about 6.0 mm NL. Some caudal neural spines and hemal spines stain with alizarin at 4.6 mm NL, and all do by 6.0 mm NL. All precaudal centra stain with alizarin by about 6.7 mm NL. All caudal centra, including the urostyle, stain with alizarin by about 7.2 mm NL. The smallest specimen in which caudal centra could be counted was 6.1 mm NL (early flexion). The second, third, and fourth dorsal rays are elongate and widely separated at the bases from preflexion (4.4 mm NL) through postflexion (12.9 mm SL). During early caudal formation (5.0 mm NL) rays near the middle of the fin begin to calcify.

Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (about 7.0 mm NL) onward. The first ray and the most posterior rays are probably calcified prior to transformation.

During early caudal formation (5.0 mm NL), anal rays near the middle of the fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from midflexion (about 6.6 mm NL) onward. The most

posterior rays are probably calcified by the time transformation is complete.

Development of the left pelvic fin precedes that of the right fin. The left pelvic fin bud appears during preflexion (before 4.5 mm NL, probably at about 4.0 mm NL). Rays develop between preflexion (about 4.5 mm NL) and postflexion (7.9 mm SL). The second ray is the first to appear (4.5 mm NL); it is elongate. (This ray may actually be the result of fusion of the second and third rays.) The first ray does not appear until early flexion (5.9 mm NL). It is weak, never elongate, and usually the shortest ray in the fin. The right pelvic fin bud appears during early flexion (5.3 mm NL). Rays develop between late flexion (6.7 mm NL) and postflexion (about 9.0 mm SL). There are five rays in the complete left fin and six in the right.

Rayless, fanlike, larval pectoral fins were present on the smallest available specimen (preflexion, 4.4 mm NL). Calcification of rays in the left fin begins during postflexion (about 11 mm SL).

Cephalic Spination

Preopercular spines (Table 4) were present in the smallest preflexion specimen (4.4 mm NL). With development (Figs. 6A, B, 7A), additional spines appear until maximum numbers of about 31 on the left side (range 25-38) and 39 on the right side (range 34-43) are reached during postflexion (8.3-10.2 mm SL). The largest specimen (12.9 mm SL) has only about three left (uncertain count) and seven right spines. Most are probably lost by transformation.

Frontal-sphenotic spines were evident in the smallest preflexion specimen (4.4 mm NL) and throughout the larval series, though less conspicuous in larger specimens (10-13 mm SL). The lowermost spine on the left side is usually just above the center of the eye and on the right side slightly anterior to the center of the eye. (During transformation those on the right side are at the anterior margin of the skull.) The spines are arranged in a slightly posteriorly concave arch following the curve of the skull. There are usually six (maximum of six) per side, including three stronger spines arising from a small bulge of the skull.

Larval Teeth (Table 5)

Numbers of teeth of preflexion (4.5-5.4 mm NL) larvae range from two upper and two lower to three upper and four lower on each side. During early caudal formation (4.6-5.3 mm NL), numbers range from two upper and three lower to three upper and four lower on each side. During early flexion (5.3-6.0 mm NL), teeth increase from two upper and four lower to four upper and five lower on each side. During midflexion (6.4-6.6 mm NL), there are four or five upper and five or six lower teeth on each side. During late flexion (6.7-7.7 mm NL), teeth increase from four upper and six lower to seven upper and eight lower on each side. During postflexion (7.9-12.9 mm SL), teeth increase from about six upper and six lower on each side to about eight upper on both sides, more than nine in the lower left jaw, and more than eight in the lower right jaw.

Transformation

Migration of the right eye may begin as early as midflexion (6.6 mm NL) or as late as postflexion (7.9 mm SL). The right eye moves from the right side of the head through a space between the dorsal fin and supraorbital bars (Fig. 7B) as in *Cyclopsetta fimbriata* (Gutherz 1971). The right eye probably reaches its final position on the left side of the head by about 18 mm SL. No early juvenile specimen was available. This size is based on a transformation rate similar to that of *Citharichthys cornutus* and a 16.0 mm SL specimen of *C. gymnorhinus* in which the right eye was about halfway to the dorsal ridge.

Occurrence

Larvae were collected in the Atlantic during February, March, April, May, and October (Powles footnote 4). There was no apparent size progression by month, indicating an extended spawning season. Water depth was 14.6-446 m. Surface temperature and salinity were 19.0°-26.5°C and 33.8-37.0‰. *Citharichthys gymnorhinus* larvae occurred slightly closer to shore and not quite as far north as those of *C. cornutus*. The reported northern limit for adult *C. gymnorhinus* is Georgia. (See *C. cornutus*, section on Occurrence.)

In the eastern Gulf of Mexico, larvae smaller than 4 mm NL were common in January, February, May, June, July, August, and November, indicating year-round spawning in that area (Dowd 1978).

Citharichthys spilopterus (Figs. 8, 9)

Identification

Most specimens had complete complements of countable characters. They were identified by comparing the following larval and juvenile counts with known adult counts. Number of specimens is given in parentheses.

Caudal fin formula = 4-5-4-4 (40)
Caudal vertebrae = 23(16), 24(38), 25(6)
Gill rakers (lower limb, first left) = 11-14 (9)
Left pelvic rays = 6 (24)
Anal rays = 55-62 (53)
Dorsal rays = 74-82 (53)

Of the potential species listed in Table 1, only 3 have 23-24 caudal vertebrae (Append. Table 1). *Citharichthys gymnorhinus* has only five left pelvic rays, and lower anal and dorsal fin ray counts. *Etropus rimosus* has 3-7 gill rakers and usually only 24-25 caudal vertebrae. In addition, most larvae were caught in an estuary, which is consistent with *C. spilopterus* adult distribution.

Distinguishing Characters

Citharichthys spilopterus larvae have no pectoral melanophore, and notochordal pigment is restricted to the caudal region. Two elongate dorsal rays are present from preflexion (3.7 mm) through transformation. Caudal vertebrae (23-24, rarely 25) can be counted by late flexion (5.7 mm). Lateral larval pigmentation is relatively light, but juvenile pigmentation is heavy. Flexion is complete at 7-8 mm SL. The larval snout is very blunt and the body is deep. Relative snout to anus length is small. The left pelvic fin has a full complement of six rays. Length at transformation is 9-11 mm. Larvae usually appear in collections from September through April.

Pigmentation

Pigmentation of *C. spilopterus* larvae is relatively light, but it becomes heavy in juveniles. Gas bladder, lower gut, and lateral tail pigment are the most striking.

By about 3.7 mm (early caudal formation, Fig. 8A) and throughout larval development, the left side of the gas bladder is fairly heavily pigmented, usually with one or two distinct melanophores. No pigment is evident on the right side of the gas bladder. Additional melanophores sometimes appear later in development, but are usually larger and fewer in number than in the preceding two species. The only other pigment apparent in the 3.7 mm specimen is a small amount along the ventral surface of the gut loop.

During late flexion (6.7 mm, Fig. 8B), two dashlike melanophores are present on the ventral body margin between the anus and the caudal fin base. A few melanophores appear on each side of the symphysis of the lower jaw. A melanophore is on the posterior margin of the articular. Pigment along the ventral surface of the gut loop increases. Some pigment may occur on the ventral body margin anterior to the cleithrum. A stellate melanophore is present at the junction of left and right branchiostegal membranes, just forward of the isthmus. A series of small melanophores usually is present along the distal tips of anal pterygiophores.

During postflexion, one to five (usually one or two) melanophores are present on the left side of the gas bladder. Additional dashlike clusters of pigment (up to four total) appear on the ventral body margin along the anal fin base, but the first two remain the most distinct (8.7 mm). Similar clusters of pigment appear on the dorsal body margin along the dorsal fin base (up to six from above the hindbrain to the caudal fin base). Heavy pigment is present along the ventral body margin anterior to the cleithrum. The area immediately around the anus is usually densely pigmented internally. Several external melanophores are present on the body below the pectoral fin base and along the ventral and lateral surfaces of the abdomen. Internal melanophores are present along the hindgut. Visible internal notochordal pigment is restricted to a small area just forward of the caudal peduncle. This appears as fine dashes along the dorsal surfaces of one to a few centra in the area of caudal vertebrae 15-16. Some internal pigment is present near the pectoral fin base and just forward of the cleithrum beneath the angle of the last gill arch (visible through the opercle). The left pelvic fin becomes pigmented, mostly around the first to third rays. Clusters of melanophores appear on the dorsal and anal fins. Often, melanophores occur along the sides of the middle caudal rays. By about 9 mm, lateral melanophores appear on the snout, jaws, and posterior part of the head. One or two internal melanophores appear above the brain.

Gas bladder pigment becomes diffuse after

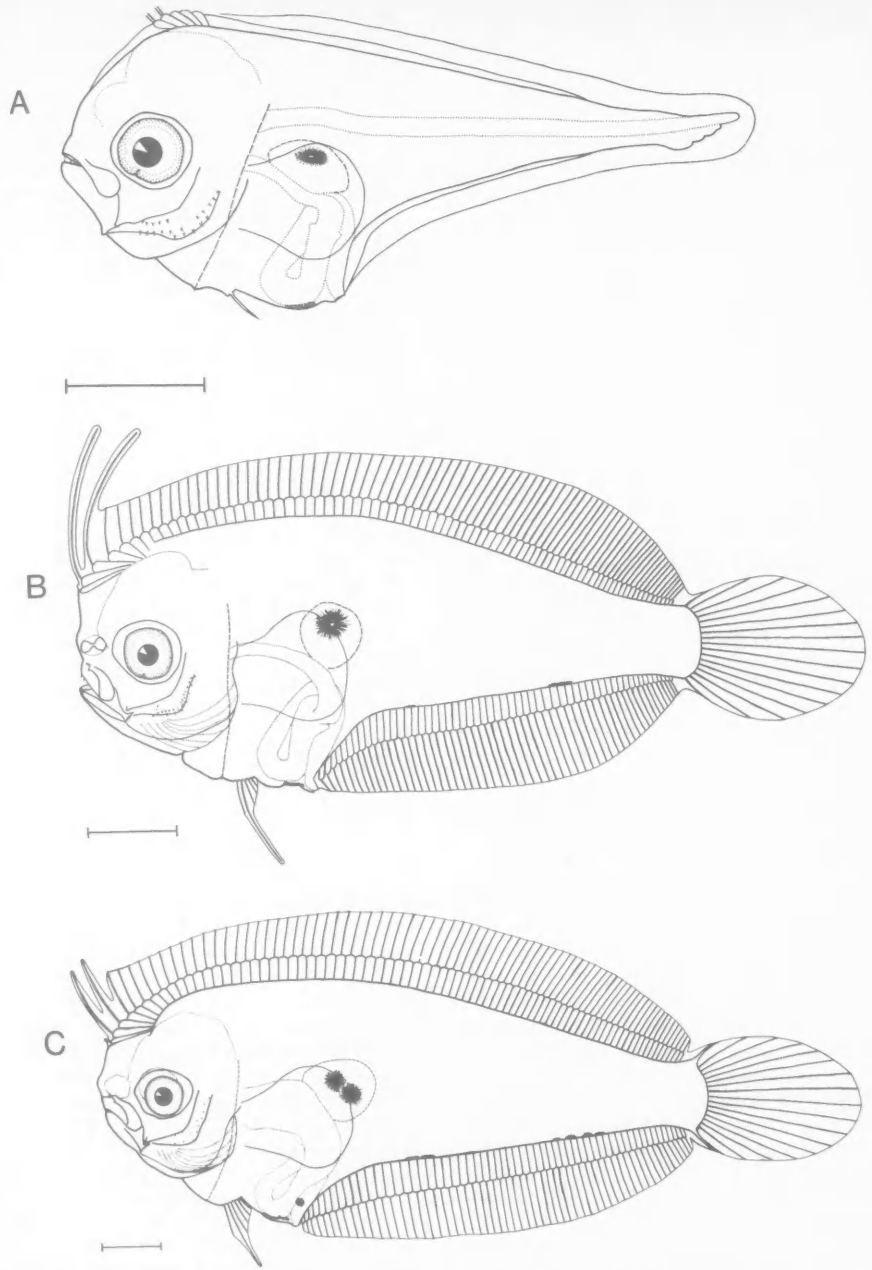


FIGURE 8.—Larval stages of *Citharichthys spilopterus*: A. Preflexion (early caudal formation), 3.7 mm; B. Late flexion, 6.7 mm; C. Transforming, 9.9 mm. Scale = 1 mm.

transformation and is obscured by body musculature in most specimens longer than 10 mm. A caudal band does not appear until the myoseptal pigment pattern of early juveniles is established (9-10 mm, Fig. 9B). By the end of transformation, myoseptal pigment is well developed, mostly adjacent to dorsal and anal pigment clusters; it often forms additional vertical bands across the body. In older juveniles (16 mm, Fig. 9C), the dorsal and anal clusters and myoseptal pigment become less distinct and partially blend in with the increasing brownish ground color.

Morphology (Figs. 8, 9; Tables 3, 7)

General morphological features are similar to those of *C. cornutus*, with the qualification that the smallest *C. spilopterus* specimen examined was 3.7 mm NL. Adult morphometrics given in the following discussion were derived from Gutherz (1967) and Dawson (1969).

During flexion and postflexion, the mouth is relatively small and is similar in size to that of *E. crossotus*. The adult mouth is also small for the genus. Upper jaw length/BL decreases greatly from 9.9% (preflexion) to 6.7% (postflexion) and then increases greatly to 9.0% (midjuvenile). Adult upper jaw length/BL is 10.5%. Upper jaw length/HL decreases greatly from 36% (preflexion) to 27-29% (flexion to early juvenile) and then increases greatly to 36% (midjuvenile). Adult upper jaw length/HL is about 37%, range 31-40%. Lower jaw length/BL decreases greatly from 12.1% (preflexion) to 9.1% (postflexion) and then increases greatly to 13.1% (midjuvenile). Adult lower jaw length/BL is 12.4%. Lower jaw length/HL decreases greatly from 43% (preflexion) to 38% (flexion and postflexion) and then increases greatly to 53% (midjuvenile). Adult lower jaw length/HL is 44%, range 41-47%.

The larval snout is relatively long but blunt. The adult snout is relatively pointed. Snout length/BL decreases from 7.5-7.6% (preflexion and flexion) to 6.4% (postflexion) and 5.0% (midjuvenile). Adult snout length/BL is 5.6%. Snout length/HL is fairly constant at 27-29% from preflexion through postflexion and then decreases to 20% (midjuvenile). Adult snout length/HL is 20%, range 18-22%.

The eye is moderate in larvae and small in adults. Eye diameter/BL decreases greatly from 9.7% (preflexion) to 6.5% (postflexion) and then increases slightly to 7.0% (midjuvenile). Postflexion eye diameter/BL is similar to those of *E. crossotus* and *E. microstomus*. Adult orbit diameter/BL is 5.6%. The large decrease in larval eye diameter/BL is exceptional among known western North Atlantic *Citharichthys* and *Etropus* larvae. Eye diameter/HL decreases greatly from 35% (preflexion) to 27-28% (postflexion to midjuvenile). Adult orbit diameter/HL is 20%, range 13-25%.

The head is very blunt, with a nearly vertical anterior profile, prior to transformation. It is relatively long during preflexion, moderate during flexion, short during postflexion, and moderate in adults. Head length/BL decreases greatly from 28% (preflexion) to 24% (postflexion) and then increases to 25% (early and midjuvenile). Adult head length/BL is 28%, range 26-31%. The decrease in relative larval head length is exceptional among known western North Atlantic *Citharichthys* and *Etropus* larvae. The head is relatively deep during preflexion and flexion, and shallow during postflexion. Head depth/BL increases from 37% (preflexion) to 39% (flexion), then decreases greatly to 33% (postflexion) and 31% (midjuvenile). Postflexion head depth/BL is similar to those of *C. gymnorhinus* and *E. crossotus*.

Snout to anus length is relatively short. Snout to anus length/BL decreases greatly from 39-40% (preflexion and flexion) to 31-32% (postflexion to midjuvenile).

The body is deep throughout the larval stages, except that the abdomen becomes only moderately deep by postflexion. During postflexion, the dorsal and ventral profiles are not as convex as in other known western North Atlantic *Citharichthys* and *Etropus* larvae. Adult body depth is moderate. Body depth at pelvic fin/BL increases from 40% (preflexion) to 47% (flexion) and then decreases to 39% (postflexion) and 35% (midjuvenile). Body depth at anus/BL increases from 39% (preflexion) to 51% (flexion) and then decreases to 43% (postflexion) and 39% (midjuvenile). Body depth at third hemal spine/BL increases from 23% (preflexion) to 41% (flexion), decreases to 37% (early juvenile), and then increases to 40% (midjuvenile). Adult body depth/BL is 46%, range 40-51%. Caudal peduncle depth/BL decreases from 14.4% (preflexion) to 13.5% (postflexion) and 11.4% (midjuvenile). Adult caudal peduncle depth/BL is 12.8%, range 11.0-13.9%. The decrease in relative larval caudal peduncle depth is exceptional among known western North Atlantic *Citharichthys* and *Etropus* larvae.

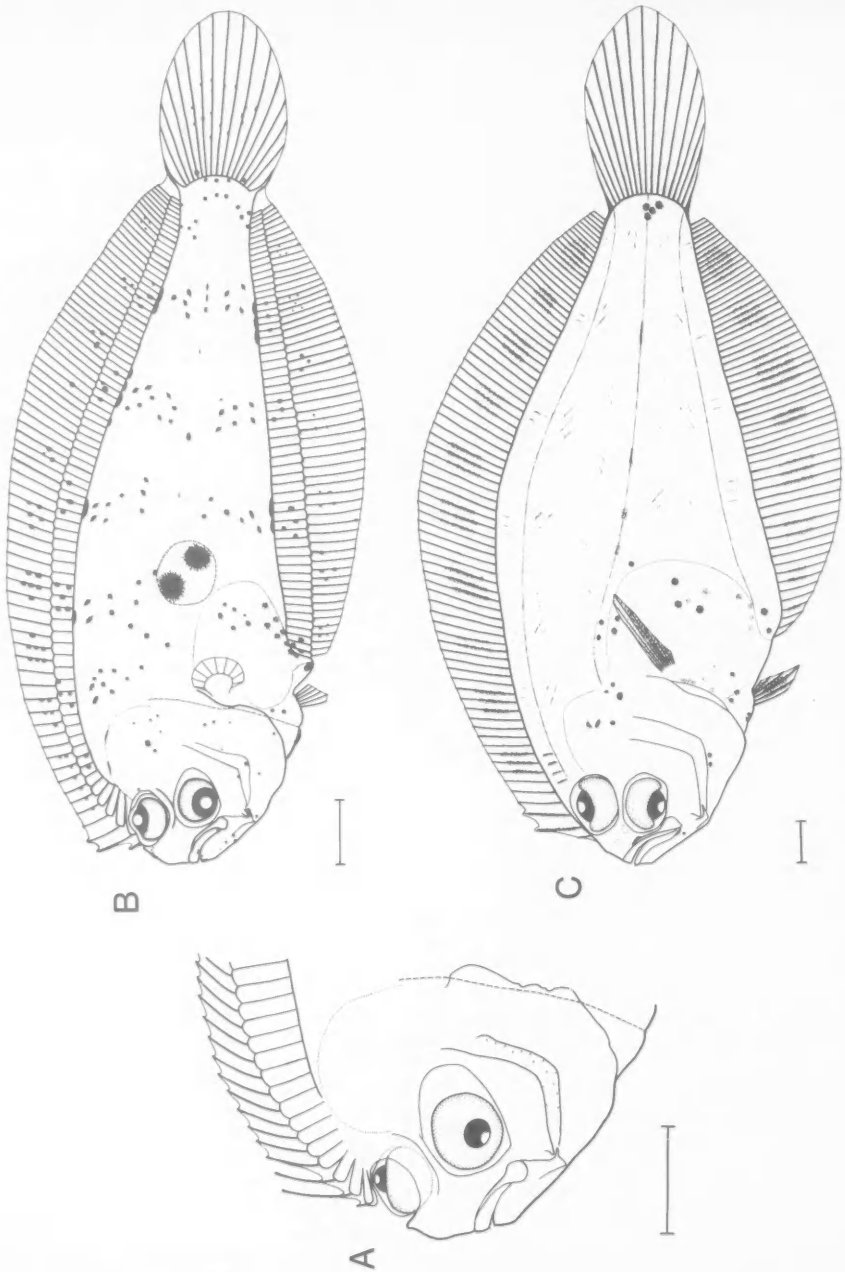


FIGURE 9.—*Citharichthys spilopterus*: A. Head of 9.9 mm larva showing migration of right eye around origin of dorsal fin (pigment omitted); B. Early juvenile, 10.7 mm; C. Juvenile, 16.6 mm. Scale = 1 mm.

TABLE 7.—Measurements (mm) of larvae and juveniles of *Citharichthys spilopterus*. ECF = early caudal formation, Late = late flexion, Post = postflexion. S = symmetrical, 1 = 0 to one-third of the way to the dorsal ridge, 2 = one-third to two-thirds of the way to the dorsal ridge, 3 = two-thirds to all the way to the dorsal ridge, R = on the dorsal ridge, T = transformed.

Body length	Upper jaw length	Lower jaw length	Snout length	Eye diameter	Head length	Snout to anus length	Total length	Head depth	Body depth at pelvic fin	Body depth at anus	Body depth at third hemal spine	Caudal peduncle depth	Flexion stage	Right eye position
3.7	0.37	0.45	0.28	0.36	1.0	1.5	3.8	1.4	[1]1.5	[1]1.4	[1]0.84		ECF	S
5.7	0.42	0.58	0.46	0.46	1.5	2.2		2.4	2.7	2.9	2.2	0.74	Late	S
6.7	0.42	0.61	0.53	0.51	1.7	2.5	8.5	2.5	3.1	3.3	2.6	0.93	Late	S
6.8	0.54	0.71	0.46	0.54	1.8	2.7		2.6	3.2	3.5	3.0	1.1	Late	1
8.3	0.66	0.80	0.55	0.53	2.0	2.7	10.4	2.8	3.4	3.7	3.2	1.2	Post	3
8.7	0.66	0.88	0.53	0.54	2.3	2.8	11.3	3.0	3.5	3.8	3.4	1.3	Post	T
8.9	0.54	0.83	0.50	0.52	2.0	3.0	11.1	3.0	3.6	4.0	3.5	1.2	Post	1
8.9	0.61	0.82	0.61	0.56	2.1	2.9	11.0	3.0	3.6	4.0	3.4	1.2	Post	2
8.9	0.65	0.85	0.50	0.63	2.2	2.9	11.1	3.1	3.5	3.8	3.4	1.3	Post	R
9.0	0.73	1.0	0.58	0.58	2.4	2.9	11.7	3.1	3.5	3.6	3.4	1.2	Post	T
9.0	0.62	0.81	0.60	0.58	2.2	2.8	11.0	3.0	3.6	4.0	3.6	1.2	Post	S
9.1	0.58	0.80	0.56	0.60	2.1	2.9	11.3	3.0	3.4	3.6	3.3	1.2	Post	3
9.1	0.70	0.90	0.65	0.60	2.4	3.1	11.2	2.9	3.3	3.4	3.1	1.2	Post	T
9.1	0.67	0.93	0.56	0.60	2.3	3.0	11.2	2.9	3.3	3.5	3.3	1.3	Post	T
9.2	0.70	0.93	0.58	0.70	2.4	2.8	11.4	3.2	3.7	3.9	3.6	1.3	Post	R
9.2	0.64	0.97	0.46	0.64	2.3	2.7	11.4	2.9	3.6	3.8	3.4	1.3	Post	T
9.2	0.67	0.87	0.60	0.62	2.4	2.8	11.4	3.0	3.6	3.8	3.5	1.3	Post	T
9.2	0.68	0.89	0.62	0.60	2.3	2.8	11.2	2.9	3.4	3.9	3.2	1.3	Post	R
9.3	0.57	0.80	0.56	0.60	2.2	2.9	11.4	3.0	3.6	3.9	3.4	1.2	Post	1
9.3	0.67	0.90	0.65	0.63	2.4	2.9	11.7	3.0	3.4	3.8	3.7	1.3	Post	T
9.4	0.68	0.93	0.53	0.68	2.4	2.7	11.7	3.0	3.5	3.7	3.4	1.3	Post	T
9.4	0.69	1.0	0.56	0.68	2.3	3.0	11.6	3.1	3.5	3.7	3.8	1.4	Post	T
9.4	0.67	0.94	0.59	0.67	2.4	2.9	11.7	2.9	3.4	3.7	3.3	1.3	Post	T
9.5	0.71	1.0	0.60	0.68	2.4	3.1	11.8	3.0	3.6	3.8	3.4	1.3	Post	T
9.6	0.66	0.91	0.71	0.53	2.3	3.1	12.0	3.3	3.8	4.1	3.8	1.4	Post	R
9.7	0.69	0.93	0.64	0.68	2.5	2.9	11.8	3.2	3.6	3.9	3.6	1.3	Post	R
9.7	0.61	0.80	0.70	0.56	2.2	3.3	11.9	3.2	3.9	4.3	3.7	1.2	Post	S
9.8	0.65	0.89	0.58	0.74	2.4	3.2	11.9	3.1	3.8	4.1	3.6	1.2	Post	1
9.8	0.67	0.87	0.70	0.64	2.4	3.2	11.9	3.1	3.8	4.4	3.8	1.2	Post	1
10.0	0.72	1.0	0.54	0.72	2.5	3.0	12.2	3.2	3.6	3.8	3.6	1.3	Post	T
10.0	0.76	1.0	0.67	0.73	2.6	3.2	12.5	3.2	3.8	3.9	3.7	1.4	Post	T
10.0		1.1		0.73	2.5	3.0	12.2	3.2	3.7	4.0	3.6	1.3	Post	T
10.2	0.68	0.90	0.70	0.67	2.4	3.2	12.4	3.2	3.9	4.2	3.8	1.3	Post	3
10.2	0.71	1.0	0.56	0.64	2.6	3.1	12.5	3.1	3.5	3.7	3.6	1.4	Post	T
10.2	0.78	1.1	0.58	0.75	2.5	3.2	12.7	3.4	3.9	4.2	3.9	1.4	Post	T
10.2	0.73	1.1	0.53	0.76	2.6	3.2	12.5	3.3	3.8	4.0	3.8	1.4	Post	T
10.2		1.0	0.60	0.70	2.4	3.2	12.2	3.3	3.9	4.1	3.9	1.4	Post	T
10.3	0.83	1.1	0.64	0.64	2.6	3.2	12.7	3.4	3.8	4.1	3.8	1.4	Post	T
10.3	0.79	1.1	0.60	0.74	2.7	3.3	13.0	3.4	3.9	4.2	3.9	1.4	Post	T
10.5	0.76	1.1	0.60	0.71	2.6	3.4	13.0	3.4	3.8	4.2	4.0	1.4	Post	T
10.5	0.59	0.92	0.60	0.66	2.4	3.2	12.9	3.5	3.9	4.4	4.2	1.4	Post	R
10.6	0.73	1.1	0.63	0.68	2.7	3.2	13.1	3.4	4.0	4.2	4.0	1.4	Post	T
10.6	0.65	1.1	0.50	0.67	2.6	3.2	13.1	3.5	4.0	4.3	4.1	1.4	Post	T
10.6	0.60	0.90	0.64	0.60	2.5	3.2	13.0	3.4	4.1	4.5	4.1	1.4	Post	1
10.7	0.74	0.95	0.47	0.77	2.6	3.2	13.0	3.2	3.8	4.1	3.9	1.4	Post	T
10.8	0.82	1.1	0.65	0.72	2.7	3.3	13.3	3.2	3.9	4.2	3.8	1.4	Post	T
10.9	0.76	1.1	0.55	0.66	2.7	3.1	13.4	3.4	4.0	4.3	4.0	1.4	Post	T
10.9	0.75	1.1	0.62	0.67	2.8	3.2	13.3	3.3	4.0	4.3	4.0	1.4	Post	T
11.0	0.81	1.1	0.61	0.65	2.7	3.2		3.4	3.8	4.0	3.9	1.3	Post	T
11.6	0.84	1.3	0.61	0.89	3.1	3.8	14.3	3.7	4.2	4.5	4.4	1.5	Post	T
14.3	1.3	1.9	0.77	1.2	3.8	4.9	18.3	4.6	5.2	5.6	5.6	1.6	Post	T
16.6	1.6	2.3	0.91	1.3	4.4	5.3	21.0	5.5	5.9	6.6	7.0	1.7	Post	T
16.7	1.5	2.2	0.75	1.1	4.0	5.0		5.2	6.0	6.4	6.6	1.9	Post	T
19.4	1.7	2.5	0.84	1.3	4.8	6.0	24.1	5.8	6.7	7.5	7.8	2.2	Post	T
22.0	2.1	3.0	1.2	1.4	5.4	6.8	27.9	6.9	7.6	8.6	9.0	2.7	Post	T
23.1	1.9	2.9	1.1	1.6	5.6	7.1	28.5	7.0	7.7	8.6	9.0	2.7	Post	T
23.3	2.1	3.1	1.2	1.6	5.8	7.2	28.9	7.2	8.4	9.2	9.4	2.8	Post	T
24.0	2.2	3.1	1.1	1.6	6.0	7.8	30.0	7.4	8.3	9.2	9.7	2.6	Post	T
25.4	2.3	3.2	1.3	1.6	6.2	8.1	31.9	7.5	8.9	9.7		3.0	Post	T

[1]Measurement does not include dorsal or anal pterygiophores.

Fin and Axial Skeleton Formation

Caudal skeleton development apparently is similar to that of *C. cornutus*. Size ranges of available larval specimens in each stage are as follows: Early caudal formation, 3.7 mm NL; late flexion, 5.7-6.8 mm NL; postflexion, 9.0-10.6 mm SL. All caudal rays are calcified by 5.7 mm.

All precaudal neural spines, the first 13 caudal neural spines, the first 13 hemal spines, and no

precaudal or caudal centra stain with alizarin at 3.7 mm NL. All neural spines and hemal spines, some precaudal centra, and the urostyle stain with alizarin at 5.7 mm NL. All precaudal and caudal centra stain with alizarin at 6.7 mm NL. The smallest specimen in which caudal centra could be counted was 5.7 mm NL (late flexion).

The second and third dorsal rays are moderately elongate and moderately separated at the bases from preflexion (3.7 mm NL) through transformation (about 10 mm SL). No other dorsal rays were formed at 3.7 mm, but adult counts were present from 5.7 mm NL onward. All dorsal rays had calcified by postflexion (8.3 mm SL).

No anal rays were formed at 3.7 mm, but adult counts were present from 5.7 mm onward. All anal rays had calcified by 8.3 mm.

The second left pelvic ray is formed by 3.7 mm; in larger specimens it is elongate. By 5.7 mm, four left and four right pelvic rays are calcified. All six rays in each fin are calcified by 6.8 mm NL.

Rayless, fanlike, larval pectoral fins were present in the smallest specimen (3.7 mm). Calcification of rays in the left fin begins during postflexion (9-10 mm SL), and is complete by the end of transformation (9-11 mm SL).

Cephalic Spination

Preopercular spines (Table 4) were present from early caudal formation (3.7 mm NL, Fig. 8A) through transformation (10.2 mm SL). Maximum numbers may be reached during or before late flexion (31 left, about 36 right); however, counts from early and midflexion larvae are lacking and those from older ones are highly variable. No preopercular spines are evident in juveniles.

The 3.7 mm NL specimen had one frontal-sphenotic spine on each side. Several postflexion (8-10 mm SL) specimens had one or two relatively inconspicuous frontal-sphenotic spines on each side. These spines may be more numerous in larvae smaller than 5.7 mm NL. None are evident in juveniles.

Larval Teeth (Table 5)

The early caudal formation (3.7 mm NL, Fig. 8A) specimen had two upper and three lower teeth on each side. During late flexion and postflexion (5.7-10.6 mm BL), larvae usually have four upper and five lower teeth on each side. Transforming larvae and early juveniles (9.1-10.7 mm SL) usually have about five upper left (probably about five upper right) and five or six lower left (probably five to eight lower right) teeth.

Transformation

Migration of the right eye may begin as early as late flexion (6.8 mm NL) or as late as postflexion (10.6 mm SL). The right eye moves from the right side of the head around the dorsal fin origin (Fig. 9A) as in *Citharichthys arctifrons* and *Etropus microstomus* (Richardson and Joseph 1973). The right eye reaches its final position on the left side of the head at about 9-11 mm SL.

Occurrence

Larvae were collected from September through December in the Gulf of Mexico off Texas (Daher[6]) and from October through April in the Cape Fear River estuary, North Carolina (pers. obs.). Temperature and salinity ranges at capture locations in the Cape Fear River were 4.1°-26.6°C and 0.0-31.7‰.

Etropus crossotus (Figs. 10, 11)

Identification

Larvae approaching transformation had complete complements of countable characters. Those specimens were identified by comparing the following larval counts with known adult counts. Number of specimens is given in parentheses.

Caudal fin formula = 4-5-4-4 (15)
Caudal vertebrae = 24(1), 25(19), 26(3)
Gill rakers (lower limb, first left) = ~7 (1)
Left pelvic rays = 6 (11)
Anal rays = 60-66 (13)
Dorsal rays = 76-84 (13)

Of the potential species listed in Table 1, only *E. crossotus* has counts that agree with these. In addition, most specimens were captured west of the Mississippi River in the Gulf of Mexico, an

[6]M. A. Daher, Graduate Student, Department of Wildlife Science, Texas A&M University, College Station, TX 77843, pers. commun. June 1978.

area from which other *Etropus* spp. have not been reported.

Distinguishing Characters

Etropus crossotus larvae have a dashlike melanophore at the base of each pectoral fin. Internal pigment along the dorsal surface of the notochord is extensive. Two elongate dorsal rays are present from preflexion (4.6 mm) through transformation. Caudal vertebrae (25-26, very rarely 24) can be counted by midflexion (5.4 mm). Lateral pigment is relatively heavy. Flexion is complete at 9-10 mm SL. The larval mouth and eye are small. The left pelvic fin has a full complement of six rays. Length at transformation is 10-12 mm. Larvae usually appear in collections from March through August.

Pigmentation

Pigmentation of *E. crossotus* larvae is relatively heavy. Pigment on the gas bladder and on the ventral and dorsal surfaces of the body is the most striking. Most useful for identification is internal pigment along the dorsal surface of the notochord and a melanophore at the base of the pectoral fin.

By about 4.6 mm (Fig. 10A) and throughout larval development, the dorsal one-third of the

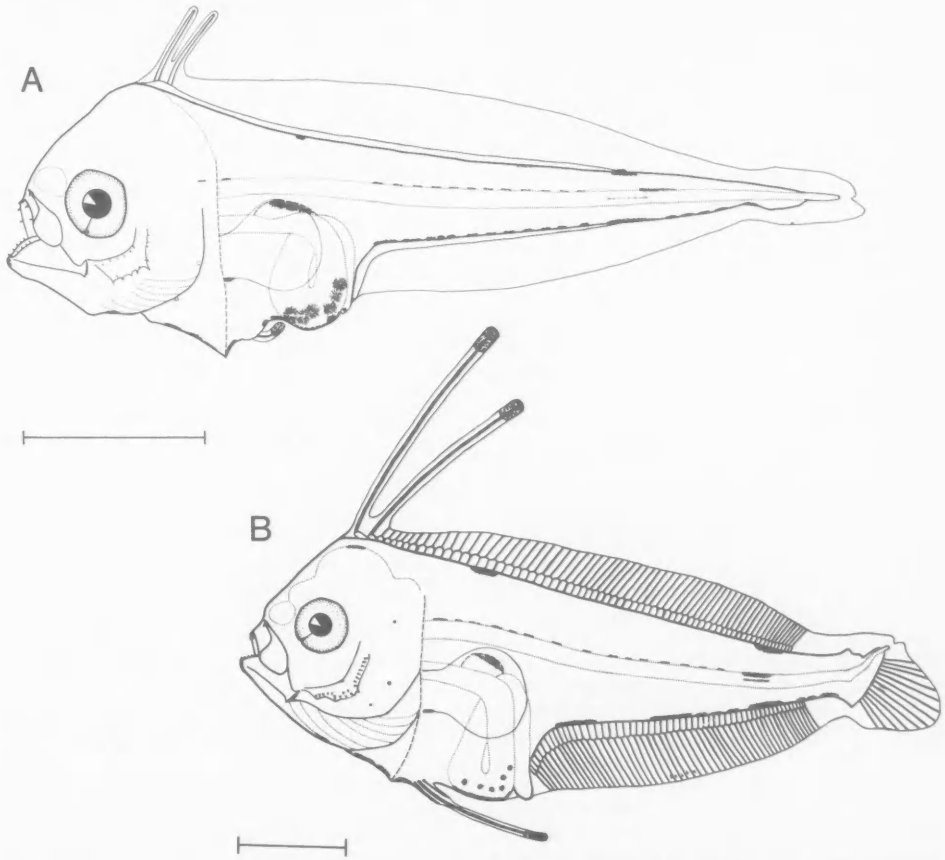


FIGURE 10.—Larval stages of *Etropus crossotus*: A. Preflexion (early caudal formation), 4.6 mm; B. Midflexion, 6.0 mm. Scale = 1 mm.

left side of the gas bladder is fairly heavily pigmented, usually with three or four distinct melanophores. The right side of the gas bladder is similarly pigmented until late flexion. Internal notochordal pigment consists of a series of fine dashes along the dorsal surface and is more extensive then in known *Citharichthys* larvae. Preflexion and early flexion larvae have up to about 12 pigment dashes between the gas bladder and caudal centrum 15. From about caudal centra 15 to 18 (range 14-20) there is a distinct series of heavy dashes which usually form a nearly solid line throughout development. An internal melanophore that appears to be associated with the notochord is located below the hindbrain near the otic capsule, where the notochord joins the brain. Dashlike clusters of pigment develop along the dorsal and ventral body margins between the pectoral fin and the caudal fin base. These clusters have not completely formed in the preflexion specimen, but three dorsal clusters and ventral pigment are present. During preflexion, a melanophore may be present on the ventral edge of the caudal finfold, opposite the midpoint of incipient hypural bones.

Throughout larval development, a continuous or broken line of pigment (the length of three to five centra) is on the lateral midline about two-thirds of the way from the anus to the notochord tip. One or two melanophores are on each side of the symphysis of the lower jaw. The posterior margin of the articular is covered with a stellate melanophore. A stellate melanophore is present at the junction of left and right branchiostegal membranes, just forward of the isthmus. About one to three internal melanophores are present near the pectoral fin base and just forward of the cleithrum beneath the angle of the last gill arch (visible through the opercle). Usually, a melanophore is on the anterodorsal edge of the urohyal. The ventral body margin between the isthmus and pelvic fin is fairly heavily pigmented with a few distinct melanophores or a continuous band of pigment. Several melanophores are present along the ventral and lateral surfaces of the abdomen and sometimes along the hindgut near the anus. The lower edge of both pectoral fin bases is lined with a dashlike melanophore. The second left pelvic ray has melanophores along its distal end. A series of small melanophores is present along the distal tips of anal pterygiophores.

During early flexion (4.9 mm), one, or rarely two, diffuse internal melanophores appear above the hindbrain.

During midflexion (5-6 mm, Fig. 10B), melanophores appear along the distal ends of the elongate dorsal rays. A group of melanophores may be present at the distal ends of the middle anal rays. Melanophores begin appearing at the bases and along the sides of middle caudal rays.

During flexion, internal notochordal pigment increases. Midflexion and late flexion larvae have up to about 5 pigment dashes between the cleithrum and gas bladder and up to about 18 dashes between the gas bladder and caudal centrum 15. From midflexion through postflexion, a small amount of pigment usually is on the anteroventral edge of the maxillary.

By late flexion (6 mm), the gas bladder has become oriented toward the left side, and greater development of musculature obscures the gas bladder from the right side. By about 8.5 mm, musculature begins to obscure notochordal pigment, except for the heavy dashes in the caudal band area. There is no evidence of a melanophore on the opercle; however, one or two small melanophores occasionally appear on the interopercle during late flexion. By about 8.5 mm, concentrations of pigment have formed around the first through third left pelvic rays. Pigment at the distal margin of the right pelvic fin appears at about the same time.

During postflexion (10.5 mm, Fig. 11A), a small melanophore appears on the upper lip. Groups of melanophores are present along the margins of dorsal and anal fins of some specimens.

In the nearly transformed specimen (10.3 mm, Fig. 11B), heavy posterior notochordal pigment is still obvious. Additional internal melanophores have appeared posterior to the hindbrain. Myoseptal pigment is well developed, mostly adjacent to dorsal and anal pigment clusters. As in *Citharichthys* larvae, this forms a caudal band. A midlateral cluster of melanophores is present near the caudal fin. Melanophores have formed along the anterior surface of the head from the snout to the dorsal fin. External and internal melanophores are present along the hindgut. Melanophores have formed along the proximal ends of groups of some dorsal and anal rays.

Morphology (Figs. 10, 11; Tables 3, 8)

General morphological features are similar to those of *Citharichthys cornutus*, with the qualification that the smallest *E. crossotus* specimen examined was 4.6 mm NL. Adult morphomet-

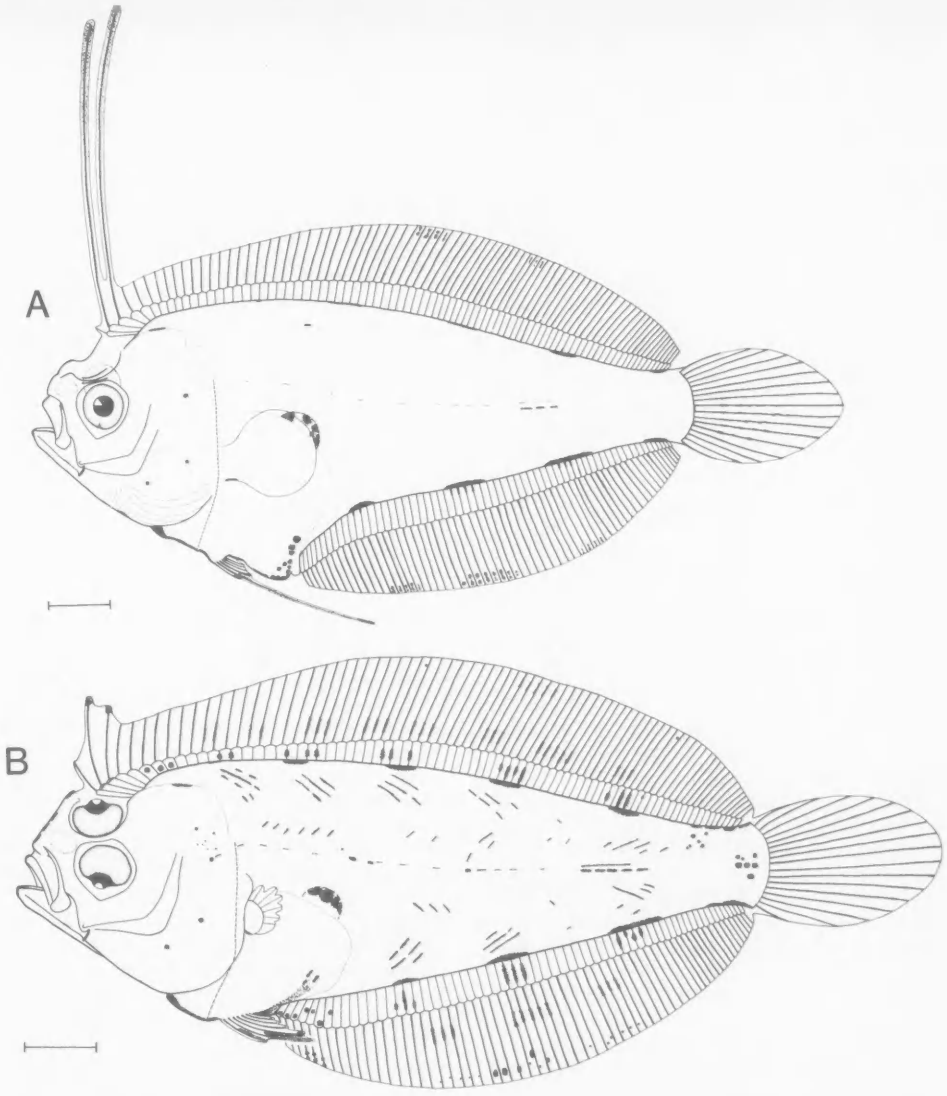


FIGURE 11.—Larval stages of *Etropus crossotus*: A. Transforming, 10.5 mm; B. Nearly transformed, 10.3 mm. Scale = 1 mm.

rics given in the following discussion are from Gutherz (1967).

The larval mouth is relatively small. During flexion and postflexion relative mouth size is similar to that of *C. spilopterus*. The adult mouth is the smallest of known western North Atlantic *Etropus* and *Citharichthys* species. Larval upper jaw length/BL is fairly constant at 7.0-7.2%. Larval upper jaw length/HL decreases from 30% to 27% (preflexion to postflexion). Adult upper jaw length/HL is 21-27%. Larval lower jaw length/BL is fairly constant at 9.6-9.8%. Larval lower

TABLE 8.—Measurements (mm) of larvae and a juvenile of *Etropus crossotus*. Pref = preflexion, ECF = early caudal formation, Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion. S = symmetrical, 1 = 0 to one-third of the way to the dorsal ridge, 2 = one-third to two-thirds of the way to the dorsal ridge, 3 = two-thirds to all the way to the dorsal ridge, T = nearly transformed.

Body length	Upper jaw length	Lower jaw length	Snout length	Eye diameter	Head length	Snout to anus length	Total length	Head depth	Body depth at pelvic fin	Body depth at anus	Body depth at third hemal spine	Caudal peduncle depth	Flexion stage	Right eye position
4.6	0.32	0.44	0.24	0.34	1.1	1.8	4.6	1.3	[1]1.2	[1]0.98	[1]0.53		ECF	S
4.9	0.35	0.43	0.27	0.37	1.2	2.1		1.6	1.6	1.4	0.89	0.23	Early	S
5.4	0.38	0.50	0.32	0.39	1.4	2.4	5.6	1.7	1.9	1.7	0.99	0.27	Early	S
5.4	0.43	0.66	0.32	0.41	1.4	2.4	6.0	1.9	2.1	1.9	1.3	0.48	Mid	S
5.5	0.40	0.53	0.40	0.36	1.4	2.5	5.8	1.9	2.0	1.8	1.3	0.43	Mid	S
5.5	0.37	0.52	0.35	0.40	1.5	2.6	6.0	1.9	2.0	1.8	1.2	0.43	Mid	S
5.6	0.43	0.57	0.33	0.40	1.4	2.4	5.9	1.8	2.1	1.9	1.3	0.37	Mid	S
5.7	0.40	0.51	0.33	0.37	1.4	2.4	5.7	1.7	1.9	1.7	1.1	0.31	Mid	S
5.7	0.35	0.49	0.29	0.35	1.4	2.4	6.0	1.8	1.9	1.8	1.2	0.35	Mid	S
5.8	0.34	0.49	0.35	0.38	1.4			1.8	1.9		1.2	0.34	Mid	S
6.0	0.43	0.56	0.40	0.42	1.6	2.7	6.5	2.0	2.2	2.1	1.4	0.43	Mid	S
6.0	0.37	0.51	0.32	0.41	1.5	2.8	6.6	2.0	3.0	1.8	1.3	0.52	Mid	S
6.0	0.50	0.62	0.42	0.43	1.6	2.8	6.8	2.1	2.4	2.2	1.6	0.53	Mid	S
6.1	0.51	0.72	0.37	0.47	1.7	2.6		2.1	2.3	2.3	1.6	0.68	Late	S
6.2	0.41	0.57	0.38	0.41	1.6	3.0	7.2	2.2	2.5	2.4	1.8	0.63	Late	S
6.9	0.50	0.67	0.47	0.46	1.9	3.2	8.2	2.3	2.8	2.6	2.0	0.73	Late	S
7.4	0.54	0.74	0.53	0.49	2.0	3.3	8.8	2.5	3.1	3.0	2.5	0.83	Late	1
8.2	0.49	0.70	0.56	0.50	2.3	3.8	10.1	2.8	3.5	3.7	3.0	1.1	Late	1
8.3	0.53	0.71	0.53	0.54	2.2	3.6	10.1	2.8	3.3	3.5	2.8	1.0	Late	S
8.3	0.63	0.78	0.53	0.54	2.2	3.6	10.1	2.9	3.5	3.8	3.2	1.1	Late	1
8.5	0.69	0.84	0.63	0.58	2.4	3.6	10.8	3.0	3.6	3.7	3.1	1.1	Late	1
9.1	0.70	0.92	0.57	0.61	2.4	3.6	11.4	3.0	3.7	3.9	3.4	1.2	Late	1
9.3	0.73	0.96	0.70	0.67	2.7	3.9		3.4	4.0	4.1	3.5	1.2	Late	1
9.3	0.64	0.84	0.63	0.65	2.6	4.0	11.9	3.4	3.8	4.1	3.6	1.2	Late	1
9.3	0.60	0.86	0.67	0.57	2.4	3.9	11.2	3.0	3.8	4.0	3.4	1.1	Post	1
9.5	0.71	0.90	0.70	0.63	2.6	4.0	11.9	3.3	4.0	4.3	3.7	1.3	Late	2
9.6	0.72	0.96	0.73	0.61	2.6	4.1	11.9	3.4	4.2	4.4	3.9	1.3	Post	1
10.3	0.80	1.1	0.75	0.71	3.0	3.4	12.7	3.3	3.7	3.7	3.7	1.2	Post	T
10.5	0.75	0.99	0.63	0.66	2.7	4.0	12.9	3.5	4.3	4.8	4.0	1.3	Post	2
10.5	0.76	1.1	0.80	0.64	2.8	4.1	12.9	3.5	4.2	4.6	4.0	1.3	Post	3
10.8	0.71	1.0	0.59		2.6	4.1	13.2	3.4	4.3	4.7	4.1	1.4	Post	1

[1]Measurement does not include dorsal or anal pterygiophores.

jaw length/HL decreases greatly from 41% to 36-37%.

The larval snout is moderate but exhibits a relatively fast growth rate. Snout length/BL increases from 5.2% to 6.8%. Snout length/HL increases from 22% to 26%.

The eye is relatively small in larvae and moderate in adults. Larval eye diameter/BL decreases from 7.4% to 6.3%. Larval eye diameter/HL decreases greatly from 32% to 24%. Adult eye diameter/HL is about 22-28%.

The larval head is of moderate length but relatively shallow depth. In adults, the head is the shortest of known western North Atlantic *Etropus* and *Citharichthys* species. Larval head length/BL increases from 23% to 26%. Adult head length/BL is 20-25%. Larval head depth/BL increases from 29% to 33-34% and is similar to that of *C. gymnorhinus*.

Larval snout to anus length is moderate. Snout to anus length/BL increases from 39% (preflexion) to 44% (flexion) and then decreases to 39% (postflexion). This length is similar to that of *C. gymnorhinus* during flexion and postflexion.

Early larvae are relatively shallow, but abdominal and tail depths increase quickly, and as adults, this species and *E. rimosus* are the deepest bodied of known western North Atlantic *Etropus* and *Citharichthys* species. During postflexion, the dorsal and ventral profiles of *E. crossotus* are relatively convex. Larval body depth at pelvic fin/BL increases greatly from 26% to 40%. Larval body depth at anus/BL increases greatly from 21% to 43% and is similar to that of *C. gymnorhinus* during flexion and postflexion. Larval body depth at third hemal spine/BL increases greatly from 12% to 38%. Adult body depth/BL is 50-58%. Larval caudal peduncle depth/BL increases from 9.6% (flexion) to 12.6% postflexion.

Fin and Axial Skeleton Formation

Caudal skeleton development is similar to that of *C. cornutus*. Size ranges of available specimens in each stage are as follows: Early caudal formation, 4.6 mm NL; early flexion, 4.9-5.4 mm NL; midflexion, 5.4-6.0 mm NL; late flexion, 6.1-9.5 mm NL; postflexion, 9.3-10.8 mm SL. Caudal rays become calcified between early flexion (4.9 mm NL) and late flexion (about 6.5 mm NL).

All precaudal neural spines stain with alizarin at 4.6 mm NL. Some caudal neural spines and hemal spines stain with alizarin at 4.6 mm NL, and all do by 5.6 mm NL. All precaudal and caudal centra stain with alizarin at about 6.0 mm NL. The urostyle stains with alizarin at 6.2 mm NL. The smallest specimen in which caudal centra could be counted was 5.4 mm NL (midflexion).

The second and third dorsal rays are elongate and moderately separated at the bases from preflexion (4.6 mm NL) through transformation (about 11 mm SL). During early flexion (4.9 mm NL), rays near the middle of the fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (about 8.0 mm NL) onward. The first ray and most posterior rays are calcified prior to transformation (by about 9.6 mm SL).

During early flexion (4.9 mm NL), anal rays near the middle of the fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (about 8.0 mm NL) onward. The most posterior rays are calcified during late flexion (about 9.3 mm NL).

Development of the left pelvic fin precedes that of the right. The left pelvic fin bud appears during preflexion (before 4.6 mm NL). Rays develop between early caudal formation (4.6 mm NL) and late flexion (8.5 mm NL). The second ray is the first to appear; it is elongate. The first ray appears soon after the second; it may be slightly elongate. The right pelvic fin bud appears during midflexion (5.5 mm NL). Rays develop between midflexion (5.8 mm NL) and late flexion (8.5 mm NL). Each complete fin has six rays.

Rayless, fanlike, larval pectoral fins are present on the smallest available specimen (4.6 mm NL). Calcification of rays in the left fin occurs during late transformation (10-11 mm SL).

Cephalic Spination

Preopercular spines (Table 4) were present in the smallest preflexion specimen (4.6 mm NL, Fig. 10A). With development (Fig. 10B), additional spines appear until maximum numbers of about 24 on the left (range 18-29) and 22 on the right (range 16-27) are reached during midflexion (5.4-6.0 mm NL). Thereafter, spines are lost until none or only a few remain at transformation (Fig. 11B).

Most specimens had three or four relatively inconspicuous frontal-sphenotic spines on each side, including one or two that were noticeably stronger.

Larval Teeth (Table 5)

The early caudal formation specimen (4.6 mm NL, Fig. 10A) had three upper and five lower teeth on each side. Early flexion larvae (4.9-5.4 mm NL) have three upper and five or six lower teeth on each side. During midflexion (5.4-6.0 mm NL), there are three to five upper and five to seven lower teeth on each side. During late flexion (6.1-9.5 mm NL), larvae usually have four upper and seven lower teeth on each side. During postflexion (9.3-10.8 mm SL), there are usually four or five upper and seven lower teeth on each side. The nearly transformed specimen (10.3 mm SL, Fig. 11B) had seven upper and more than nine lower teeth on each side.

Transformation

Migration of the right eye may begin as early as late flexion (7.4 mm NL) or as late as postflexion (10.8 mm SL). The right eye moves from the right side of the head around the dorsal fin origin (Fig. 11A) as in *C. arctifrons* and *E. microstomus* (Richardson and Joseph 1973). The right eye reaches its final position on the left side of the head at about 10-12 mm SL.

Occurrence

Larvae were collected in the Cape Fear River Estuary during May (pers. obs.) and in the Gulf of Mexico off Louisiana west of the Mississippi River Delta during July and August (Walker[7]). Moe and Martin (1965) suggested a spawning season from March to at least June for the eastern Gulf of Mexico off Florida (based on ripe

[7]H. J. Walker, Research Technician, North Carolina State University, Cape Fear Estuarine Laboratory, P.O. Box 486, Southport, NC 28461, pers. commun. July 1977.

females). Capture of a ripe female from the same area in June was reported by Topp and Hoff (1972). Christmas and Waller (1973) suggested that spawning may be nearly continuous throughout the year. However, that observation was partly based on the occurrence of one juvenile specimen during January and another during February that could have been spawned in the late summer or early fall. Therefore, the season may extend beyond August, but the evidence is not yet complete.

Comparisons

Larval Characters

Morphology seems to be influenced by the environment and duration of larval existence. *Citharichthys cornutus* and *C. gymnorhinus* are found in deeper water and may have longer pelagic larval stages than *C. spilopterus* or *E. crossotus*. In some respects, the latter two species are similar to each other and dissimilar to the first two. *Citharichthys spilopterus* and *E. crossotus* have only two elongate dorsal rays, as opposed to three in the other two species. They have smaller, less conspicuous frontal-sphenotic spines, and fewer larval teeth. (However, the jaws of *C. spilopterus* later grow at a relatively fast rate and acquire correspondingly more adult teeth.) During transformation, the origin of the dorsal fin is slightly farther forward relative to the right eye in *C. cornutus* and *C. gymnorhinus* than in the other two species. (However, after transformation the dorsal origin is more anterior relative to the right eye in all three *Citharichthys* species than in *E. crossotus*.) *Citharichthys spilopterus* and *E. crossotus* larvae have smaller eyes and mouths than the other two. They also complete transformation at a smaller size.

Known similarities among *Citharichthys* larvae that are not shared with *Etropus* larvae include the absence of a pectoral melanophore (except possibly in *C. macrops*), less extensive internal notochordal pigmentation, and, later, more gill rakers. Except for a shallower body and smaller eyes, *C. arctifrons* larvae are morphologically similar to those of *C. cornutus* and *C. gymnorhinus*. *Etropus microstomus* larvae are similar to those of *E. crossotus*.

Larval Occurrence

Differences among distributions of larvae (Append. Table 5) can be helpful in identifying them to species. Months of occurrence of larvae reported here are those in which larvae have been collected throughout the ranges of the respective species (except that data for *C. macrops* are from the southern part of its range, and data for *C. arctifrons* and *C. arenaceus* are from the northern parts of their ranges). Because most sampling was not continuous throughout the year, presence in other months is not precluded; however, enough is known to delineate approximate spawning seasons for most of the species. Larval occurrence of *C. cornutus*, *C. gymnorhinus*, *C. spilopterus*, and *E. crossotus* was discussed in the earlier species' accounts.

Throughout their ranges, *E. microstomus* spawns from March through August and *E. rimosus* spawns from September to April (Leslie 1977). Leslie suggested that spawning of the two species may be temporally distinct. This conflicts with spawning of *E. microstomus* reported from May to December (Richardson and Joseph 1973), and my information is not sufficient to resolve this conflict. However, Scherer and Bourne (1980) collected *E. microstomus* eggs in September and larvae in October in Block Island Sound, which is north of the reported adult range (Table 1). In the eastern Gulf of Mexico, larvae of *E. rimosus* smaller than 4 mm NL were common in November, January, February, and May (Dowd 1978).

Small juveniles (≥13 mm SL) of *C. abbotti* were caught in the Gulf of Mexico from Veracruz to Campeche, Mexico, in June and September (Dawson 1969), indicating a spawning season approximately from May through August, or longer.

Citharichthys macrops larvae smaller than 4 mm NL were caught in the eastern gulf in May and November (Dowd 1978). Topp and Hoff (1972) reported juveniles from the same part of the gulf during the fall and winter. The season probably extends from May through November, and possibly longer.

Richardson and Joseph (1973) reported a spawning season approximately from May to December for *C. arctifrons* in the Chesapeake Bight, with peak spawning from July through October.

Dawson (1969) reported a 27 mm SL specimen of *C. arenaceus* caught in the British West Indies in November. This may indicate summer spawning, probably during August or September at least.

Citharichthys amblybregmatus and *C. dinoceros* are deepwater forms. Because of the constancy of their environment, they may have extended spawning seasons, but little is known of their habits.

Considering the geographic and bathymetric distributions of adults (Table 1) and probable spawning periods (Append. Table 5), it is unlikely that large numbers of larvae of different species of western North Atlantic *Citharichthys* and *Etropus* cooccur in the ichthyoplankton at any given time. Among the six deepwater species, *C. amblybregmatus* and *C. dinoceros* larvae probably occur relatively far from shore. Apparently, there is little difference between larval occurrence of *C. gymnorhinus* and *C. cornutus*, but spawning centers or peak periods could be distinct. Topp and Hoff (1972) suggested that adults of the two species were bathymetrically separated, *C. gymnorhinus* being found in shallower water. *Etropus rimosus* adults occur in shallow water and do not spawn during the summer. *Citharichthys arctifrons* has a more northern distribution than the preceding three species and its spawning peak is in the summer, probably earlier than that of *E. rimosus*. Among the three coastal species, the geographic range of *C. arenaceus* is distinct from those of the other two, and *C. macrops* and *E. microstomus* cooccur only off the Carolinas. In this area of overlap, *C. macrops* probably spawns in the fall and *E. microstomus* in the spring. Among the three estuarine and coastal species, *C. abbotti* spawns in the warmer months and may be restricted to very shallow water. *Citharichthys spilopterus* spawns in the colder months, beginning in late summer in the Gulf of Mexico and in mid to late fall off the Carolinas. *Etropus crossotus* may spawn from March through the summer, or later, in the gulf, but probably does not begin off the Carolinas until after most spawning activity of *C. spilopterus* is finished.

SUMMARY

The caudal fin formula (4-5-4-4) is the most reliable character for linking larval specimens to the group of paralichthyine genera *Citharichthys*, *Cyclopsetta*, *Etropus*, and *Syacium*.

The most useful characters for identification to genus are number of elongate dorsal rays, degree of cephalic spination, and pigmentation. Known western North Atlantic *Syacium* and *Cyclopsetta* larvae have 5-10 elongate dorsal rays and well-developed preopercular and frontal-sphenotic spines. Known western North Atlantic *Citharichthys* larvae have two or three elongate dorsal rays, small (or no) preopercular spines, small frontal-sphenotic spines, no pectoral melanophore (except possibly *C. macrops*), little notochordal pigmentation, usually large eyes and mouths, and (except for *C. arctifrons*) high gill raker counts. Known western North Atlantic *Etropus* larvae have no or two elongate dorsal rays, small preopercular and frontal-sphenotic spines, a melanophore at the base of the pectoral fin, extensive notochordal pigmentation, small eyes, and low gill raker counts.

Table 9 summarizes the most useful characters for distinguishing larvae of the six species of western North Atlantic *Citharichthys* and *Etropus* that have been described in detail. The best characters for determining species are number of elongate dorsal rays, number of caudal vertebrae, pectoral and notochordal pigmentation, number of left pelvic rays (*C. gymnorhinus*), head shape and snout to anus length (*C. spilopterus*), number of gill rakers, and length at transformation.

Citharichthys arctifrons larvae have three elongate dorsal rays, no preopercular spines, many caudal vertebrae, a small eye, large mouth, and few gill rakers. *Citharichthys cornutus* larvae have three elongate dorsal rays, a strong first left pelvic ray, heavy pigmentation, a large eye and mouth, and relatively many gill rakers. *Citharichthys gymnorhinus* larvae have three elongate dorsal rays, few caudal vertebrae, five left pelvic rays (with the first weak), a distinct caudal pigment band, large eye and mouth, and relatively many gill rakers. *Citharichthys spilopterus* larvae have two elongate dorsal rays, few caudal vertebrae, little pigmentation, a small eye and mouth, very blunt anterior profile, short snout to anus length, and relatively many gill rakers.

Etropus crossotus larvae have two elongate dorsal rays, heavy pigmentation, a small eye and mouth, and many (for the genus) gill rakers. *Etropus microstomus* larvae have no elongate dorsal rays, a small eye, and few gill rakers.

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TABLE 9.—The most useful characters, in order of ontogenetic appearance, for distinguishing larvae of four species of *Citharichthys* and two species of *Etropus*.

Character	*C. arctifrons*[1]	*C. cornutus*	*C. gymnorhinus*	*C. spilopterus*	*E. crossotus*	*E. microstomus*[1]
Pectoral melanophore (before transformation)	Absent	Absent	Absent	Absent	Present	Present
Notochordal pigment (before transformation)	Caudal only	Caudal only	Caudal only	Caudal only	From brain to caudal area	From brain to caudal area
Elongate dorsal rays (before transformation)	3	3	3	2	2	0
Caudal vertebrae	26-28	25-26	23-24	[2]23-24(25)	[2](24)25-26	[2]24-25(26)
Lateral pigment (before transformation)	Moderate	Heavy	Moderate	Light	Heavy	Moderate
Length at flexion (mm)	9	9-10	7-8	7-8	9-10	7
Left pelvic rays (full complement)	6	6	5	5	6	6
Left preopercular spines (during preflexion-flexion-postflexion)	0	14-31-22	17-22-31	31-31-16	17-20-11	Several
Eye diameter/BL in % (during preflexion-flexion-postflexion)	7	10-10- 8	9- 9- 9	10- 8- 7	7- 7- 6	7
Upper jaw length/BL in % (during preflexion-flexion-postflexion)	10	10-11-10	10- 9- 9	10- 7- 7	7- 7- 7	9
Lower jaw length/BL in % (during preflexion-flexion-postflexion)		13-14-13	12-13-13	12-10- 9	10-10-10	
Snout to anus length/BL in % (during preflexion-flexion-postflexion)	42	46-46-39	43-44-40	40-39-32	39-44-39	40
Gill rakers on the lower limb of the first arch (at transformation)	6- 8	10-15	9-14	9-15	6- 9	4- 7
Length at transformation (mm)	13-15	~18	~18	9-11	10-12	10-12
Snout spine (at about transformation)	May be present	Present (in males?)	Present (in males?)	Absent	Absent	Absent
Symphyseal spine (after transformation)	Absent	Present (in males?)	Present (in males?)	Absent	Absent	Absent

[1]Data for *C. arctifrons* and *E. microstomus* are mostly from Richardson and Joseph (1973).
[2]Uncommon counts given in parentheses.

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LITERATURE CITED

AMAOKA, K.
1969. Studies on the sinistral flounders found in the waters around Japan—Taxonomy, anatomy and phylogeny. J. Shimoneseki Univ. Fish. 18:65-340.

CHRISTMAS, J. Y., AND R. S. WALLER.
1973. Estuarine vertebrates, Mississippi. *In* J. Y. Christmas (editor), Cooperative Gulf of Mexico estuarine inventory and study, Mississippi, p. 320-403. Gulf Coast Res. Lab., Ocean Springs, Miss.

DAWSON, C. E.
1969. *Citharichthys abbotti*, a new flatfish (Bothidae) from the southwestern Gulf of Mexico. Proc. Biol. Soc. Wash. 82:355-372.

DOWD, C. E.
1978. Abundance and distribution of Bothidae (Pisces, Pleuronectiformes) larvae in the eastern Gulf of Mexico, 1971-72 and 1973. M.S. Thesis, Univ. Miami, Miami, 106 p.

EVSEENKO, S. A.
1979. Larvae of the flounder *Cyclopsetta* Gill, 1888 (Bothidae, Pisces) from the northwestern Atlantic. Biol. Morya 1979(2):67-75.

FAHAY, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.

FUTCH, C. R.
1977. Larvae of *Trichopsetta ventralis* (Pisces: Bothidae), with comments on intergeneric relationships within the Bothidae. Bull. Mar. Sci. 27:740-757.

FUTCH, C. R., AND F. H. HOFF, JR.
1971. Larval development of *Syacium papillosum* (Bothidae) with notes on adult morphology. Fla. Dep. Nat. Resour. Mar. Res. Lab., Leafl. Ser., Vol. IV, Pt. 1, No. 20, 22 p.

GOODE, G. B., AND T. H. BEAN.
1896. Oceanic ichthyology. U.S. Natl. Mus., Spec. Bul`., 553 p.

GUTHERZ, E. J.
1967. Field guide to the flatfishes of the family Bothidae in the western North Atlantic. U.S. Fish Wildl. Serv., Circ. 263, 47 p.
1970. Characteristics of some larval bothid flatfish, and development and distribution of larval spotfin flounder, *Cyclopsetta fimbriata* (Bothidae). U.S. Fish Wildl. Serv., Fish. Bull. 68:261-283.

GUTHERZ, E. J., AND R. R. BLACKMAN.
1970. Two new species of the flatfish genus *Citharichthys* (Bothidae) from the western North Atlantic. Copeia 1970:340-348.

HENSLEY, D. A.
1977. Larval development of *Engyophrys senta* (Bothidae), with comments on intermuscular bones in flatfishes. Bull. Mar. Sci. 27:681-703.

HSIAO, S. C. T.
1940. A new record of two flounders, *Etropus crossotus* Goode and Bean and *Ancylopsetta dilecta* (Goode and Bean), with notes on postlarval characters. Copeia 1940:195-198.

LESLIE, A. J., JR.
1977. The systematics of *Etropus microstomus* (Gill) and *E. rimosus* Goode and Bean (Pisces: Bothidae), with ecological notes. M.S. Thesis, Florida State Univ., Tallahassee, 81 p.

MOE, M.A., JR., AND G. T. MARTIN.
1965. Fishes taken in monthly trawl samples offshore of Pinellas County, Florida, with new additions to the fish fauna of the Tampa Bay area. Tulane Stud. Zool. 12: 129-151.

MOSER, H. G., E. H. AHLSTROM, AND E. M. SANDKNOP.
1977. Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 402, 71 p.

PIETRAFESA, L. J., J. O. BLANTON, AND L. P. ATKINSON.
1978. Evidence for deflection of the Gulf Stream at the Charleston Rise. Gulfstream 4(9):3-7.

RICHARDSON, S. L., AND E. B. JOSEPH.
1973. Larvae and young of western North Atlantic bothid flatfishes *Etropus microstomus* and *Citharichthys arctifrons* in the Chesapeake Bight. Fish. Bull., U.S. 71:735-767.

SCHERER, M. D., AND D. W. BOURNE.
1980. Eggs and early larvae of smallmouth flounder, *Etropus microstomus*. Fish. Bull., U.S. 77:708-712.

SMITH, W. G., J. D. SIBUNKA, AND A. WELLS.
1975. Seasonal distributions of larval flatfishes (Pleuronectiformes) on the continental shelf between Cape Cod, Massachusetts, and Cape Lookout, North Carolina, 1965-66. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-691, 68 p.

SUMIDA, B. Y., E. H. AHLSTROM, AND H. G. MOSER.
1979. Early development of seven flatfishes of the eastern North Pacific with heavily pigmented larvae (Pisces, Pleuronectiformes). Fish. Bull., U.S. 77:105-145.

TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596), 17 p.

TOPP, R. W., AND F. H. HOFF, JR.
1972. Flatfishes (Pleuronectiformes). Mem. Hourglass Cruises, 4 (Pt. 2), 135 p.

WENNER, C. A., C. A. BARANS, B. W. STENDER, AND F. H. BERRY.
1979. Results of MARMAP otter trawl investigations in the South Atlantic Bight. I. Fall 1973. S.C. Mar. Resour. Cent., Tech. Rep. 33, 79 p.

APPENDIX TABLE 1.—Frequency distributions of caudal vertebral counts for western North Atlantic species of *Citharichthys* and *Etropus*.[1]

Species	21	22	23	24	25	26	27	28	29	*N*	$\bar{X}$
C. abbotti	19	96	9							124	21.92
C. arenaceus	3	38	8							49	22.10
C. gymnorhinus			9	27						36	23.75
C. spilopterus			23	109	8					140	23.89
E. rimosus			3	50	53	5				111	24.54
E. microstomus				51	61	2				114	24.57
C. macrops				27	46					73	24.63
E. crossotus				1	69	15				85	25.16
C. cornutus					15	29				44	25.66
C. amblybregmatus					5	16				21	25.76
C. arctifrons						5	34	3		42	26.95
C. dinoceros						([2])			([2])		

[1]Compiled from Gutherz 1967; Dawson 1969; Gutherz and Blackman 1970; Leslie 1977; S. L. Richardson, Research Assistant Professor, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. December 1976 (unpubl. data for *E. microstomus* and *C. arctifrons*); and original data for larvae, juveniles, and adults of *C. gymnorhinus, C. spilopterus, C. macrops, E. crossotus,* and *C. cornutus.*
[2]Extremes of counts.

APPENDIX TABLE 2.—Frequency distributions of anal fin ray counts for western North Atlantic species of *Citharichthys* and *Etropus*.[1]

Species	48	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	76	*N*	$\bar{X}$
C. arenaceus	([2])		1	11	8	14	9	3																	46	53.6
E. microstomus		([2])	1	1	2	8	14	22	32	31	23	15	6	5	([2])										160	57.5
C. gymnorhinus			2		4	3	3	9	13	6	10	3	2												55	56.8
C. abbotti				1	5	13	37	35	22	14	4	1													132	55.9
E. rimosus					1	5	5	17	25	42	57	57	38	41	16	6	1								311	59.5
C. spilopterus							([2])	15	24	30	41	26	11	4	([2])										151	58.6
C. macrops								1	1	6	2	5	17	16	13	12									73	61.6
E. crossotus										1	1	1	6	10	12	13	13	3		([2])					60	63.2
C. arctifrons										([2])		1	1	7	6	10	23	16	8	6	2	2	1		83	65.3
C. cornutus											([2])	3	2	7	4	6	5	1	1						27	63.0
C. amblybregmatus															1	3	2	3	1	9		1	2		22	67.0
C. dinoceros																						([2])		([2])		

[1]Compiled from Gutherz 1967; Dawson 1969; Gutherz and Blackman 1970; Topp and Hoff 1972; Leslie 1977; S. L. Richardson, Research Assistant Professor, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. December 1976 (unpubl. data for *C. arctifrons*); and original data for juveniles and adults of *C. gymnorhinus, C. spilopterus, C. macrops, E. crossotus,* and *C. cornutus.*
[2]Extremes of counts, not included in totals.

APPENDIX TABLE 3.—Frequency distributions of dorsal fin ray counts for western North Atlantic species of *Citharichthys* and *Etropus*.[1]

Species	67	68	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	90	95	*N*	$\bar{X}$
E. microstomus	([2])	2	1	2	7	8	22	21	26	24	23	12	6	4	1	1	([2])						160	76.1
C. arenaceus		([2])	1	2	11	10	9	7	3	2													45	73.5
C. gymnorhinus			7	8	12	9	8	5	3	1													53	72.7
E. rimosus			2		8	16	18	43	57	52	48	40	17	4	4	1							310	76.7
C. abbotti					1	5	13	23	30	23	23	11	2	1									132	76.4
C. spilopterus						1	4	4	14	35	32	24	26	11	5	1		1					158	78.3
C. cornutus							1	1	1	3	5	8	6	5	1	1	1						33	79.2
C. macrops							1	1	1	1		3	9	10	12	12	11	8	3				72	82.1
C. arctifrons								1	1	3	8	8	14	14	17	7	2	3	3	2			83	81.0
E. crossotus								([2])	3	2	8	12	10	11	8	6			1	([2])			61	80.1
C. amblybregmatus											2	3	1	2	6	3	2	1	2				22	81.9
C. dinoceros																					([2])	([2])		

[1]Compiled from Gutherz 1967; Dawson 1969; Gutherz and Blackman 1970; Topp and Hoff 1972; Leslie 1977; Sopher, T. R., a meristic and morphometric study of geographic populations of *Etropus microstomus*. Unpubl. manuscr., 5 p., Virginia Institute of Marine Science, Gloucester Point, VA 23062; S. L. Richardson, Research Assistant Professor, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. December 1976 (unpubl. data for *C. arctifrons*); and original data for juveniles and adults of *C. gymnorhinus, C. spilopterus, C. cornutus, C. macrops,* and *E. crossotus.*
[2]Extremes of counts, not included in totals.

APPENDIX TABLE 4.—Ranges of number of gill rakers on the lower limb of the first arch for western North Atlantic species of *Citharichthys* and *Etropus*.[1]

Species	Range	Species	Range
E. rimosus	3-7	*C. spilopterus*	9-15
E. microstomus	4-7	*C. cornutus*	10-15
C. arctifrons	6-8	*C. arenaceus*	12-15
E. crossotus	6-9	*C. macrops*	12-16
C. dinoceros	7-10	*C. abbotti*	13-16
C. gymnorhinus	9-14	*C. amblybregmatus*	18-24

[1]Compiled from Gutherz 1967; Dawson 1969; Gutherz and Blackman 1970; and Topp and Hoff 1972.

APPENDIX TABLE 5.—Probable spawning seasons of seven species of *Citharichthys* and three species of *Etropus*.[1] Estuarine = usually found in estuaries and shallow coastal waters < 40 m; Shallow = usually found in shallow coastal waters < 40 m, rarely in estuaries; Intermediate = usually found at 30-140 m depths, rarely shallower; Deep = usually found deeper than 140 m, seldom shallower.

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Adults occur	Larvae occur
C. gymnorhinus	×	×	×	×	×	×	×	×		×	×		Intermediate	Offshore
C. cornutus	×	×	×	×	×	×	×	×		×	×		Deep	Offshore
E. crossotus			×	×	×	×	×	×					Estuarine	Offshore and in estuaries
E. microstomus			×	×	×	×	×	×	×				Shallow	Offshore
C. abbotti					+	+	+	+					Estuarine	?
C. macrops					×	+	+	+	+		×		Shallow	Offshore
C. arctifrons					×	×	×	×	×	×	×	×	Intermediate (and Deep)	Offshore
C. arenaceus									+				Shallow	?
C. spilopterus	×	×	×	×					×	×	×	×	Estuarine	Offshore and in estuaries
E. rimosus	×	×	×	×	×				×	×	×	×	Intermediate	Offshore
C. amblybregmatus						?							Deep	Offshore?
C. dinoceros						?							Deep	Offshore?

[1]Compiled from Dawson 1969; Topp and Hoff 1972; Richardson and Joseph 1973; Leslie 1977; Dowd 1978; Scherer and Bourne 1980; and unpublished data from collections of South Carolina Marine Resources Research Institute, Louisiana State University, North Carolina State University, and Texas A&M University. × = times based on collections of larvae and ripe females, + = times based on collections of juveniles.

AVOIDANCE OF TOWED NETS BY THE EUPHAUSIID *NEMATOSCELIS MEGALOPS*[1]

P. H. WIEBE,[2] S. H. BOYD,[2] B. M. DAVIS,[2] AND J. L. COX[3]

ABSTRACT

Avoidance of towed nets by the common oceanic euphausiid crustacean *Nematoscelis megalops* was studied by comparing aspects of its sampling distribution as revealed by day and night catches of two nets of different size, one with a 1 m^2 mouth opening and one with a 10 m^2 opening. Both nets yield essentially the same pattern in vertical distribution. Paired tows yield a highly significant agreement in nighttime abundance estimates, but do not give comparable daytime estimates. Night catches, especially with the smaller net, exceed day catches, an effect which is interpreted as resulting from greater avoidance during the day. Comparisons between nets show that neither size net has a superior catch rate, day or night. No particular size group of the species is caught with greater efficiency by either net. When *N. megalops*' center of distribution is shallower, differences between day and night catches can be substantially enhanced.

Application of Barkley's avoidance theory indicates that the potential advantage of greater mouth area of the larger net is effectively cancelled by individuals reacting to the approach of the net at a greater distance. Other theoretical predictions which depend upon the assumption of increasing escape velocities as a function of body size are not corroborated by the field data. Thus, field population size-frequency distributions are probably not materially affected by avoidance.

The evidence suggests that *N. megalops* uses vision to detect the net approach. Net contrast with the background due to down-welling light during the day and bioluminescence produced in and around the net both day and night appear to be the most likely stimuli. Future efforts to reduce net avoidance by species like *N. megalops* must focus on reduction of these signals.

Avoidance of capture by towed nets is a major source of underestimation bias associated with zooplankton abundance measurements (Clutter and Anraku 1968; Wiebe and Holland 1968; Wiebe 1971). This factor is perhaps the most important determinant of the accuracy of abundance estimates for some of the larger zooplankton species. Patchiness of zooplankton may cause large differences between successive tows taken at a single station (Wiebe 1971; Wiebe et al. 1973), but the error induced by this factor is not comparable with avoidance error, since patchiness "error" is essentially unbiased. The precision of the estimate of abundance for a particular station location will improve with greater sample numbers, but avoidance error will persist as an underestimation bias. Since patchiness of zooplankton exists on scales from the microscale (centimeters to meters) to the mesoscale (hundreds of kilometers) (Mackas and Boyd 1979; Haury et al. 1978), patchiness itself can be viewed not as a sampling problem, but rather as a reflection of natural distributions. Avoidance and technical problems such as clogging and escapement (Vannucci 1968) represent sampling biases which tend to obscure our picture of these natural distributions. Although clogging and escapement are still important sources of error, improved net design can, in many instances, eliminate these as major problems (Smith et al. 1968). Zooplankton avoidance of nets, at least for some species, remains as an important sampling problem.

Avoidance is variable, depending upon such factors as time of day; light regime; size, shape, and color of the net; speed of tow; species; sex or developmental stage of the organisms; their physiological state; and absolute density (Fleminger and Clutter 1965; Isaacs 1965; McGowan and Fraundorf 1966; Brinton 1967; Clutter and Anraku 1968; Laval 1974; Boyd et al. 1978). Almost certainly this diversity of factors is one of the major reasons for a lack of consensus regarding the extent or magnitude of avoidance bias for

[1]Contribution No. 4796 from the Woods Hole Oceanographic Institution, Woods Hole, Mass.

[2]Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

[3]Oceanic Biology Group, Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA 93106.

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any particular zooplankton group. Further, the mechanisms by which an oncoming net is detected and avoided are not well known (Clutter and Anraku 1968).

Theoretical studies of avoidance (Barkley 1964, 1972; Clutter and Anraku 1968; Murphy and Clutter 1972; Laval 1974) have drawn attention to important behavioral aspects of avoidance and how these behavioral features are likely to interact with net size and towing speed. Avoidance theory provides a framework for the design of avoidance field studies and the interpretation of their results, as Barkley's (1972) examples clearly demonstrated. We have applied avoidance models to data on the euphausiid *Nematoscelis megalops* to determine its response to different net types under different conditions. Since our data on this relatively abundant species indicated substantial avoidance effects, we have examined it in some detail.

In studies of *N. megalops* vertical distributions (Wiebe and Boyd 1978; Boyd et al. 1978) night tows were consistently observed to produce higher numerical density estimates than tows at the same station during the day. These tows were taken with a multiple net system with a 1 m^2 mouth opening (MOCNESS, Wiebe et al. 1976). Although horizontal patchiness may have contributed in an unbiased way to the day/night differences in catch rate, the overall comparison of day and night tows strongly suggested greater avoidance during the day. Unfortunately, there were too few day/night pairs at a single station to demonstrate this by pairwise comparison.

During 1976 and 1977, as part of a multidisciplinary study of Gulf Stream cold core rings (Lai and Richardson 1977; Richardson 1980), more complete observations of day/night vertical distributions were made at stations in Slope Water and cold core rings. Tows were taken with a 1 m^2 MOCNESS and with a 10 m^2 MOCNESS. As will be demonstrated below, both net systems catch *N. megalops* without apparent size discrimination between the two. Both net systems are avoided to a certain extent, based on day/night catch ratios, but some revealing differences are evident. Using data from both sizes of nets, it is possible to apply Barkley's (1972) avoidance model to obtain independent estimates of the parameters of reaction distance and percent capture within a certain animal size range, and through a comparative analysis reach some tentative conclusions regarding avoidance mechanisms in the species studied.

METHODS

The combinations of 1 m^2 and 10 m^2 MOCNESS tows were taken at nine stations (Fig. 1), with additional information about each tow in Table 1. Stations 1-4 were sampled in April 1977 on RV *Knorr* cruise 65 and stations 5-9 were sampled on *Knorr* 71. Station 1 was in cold core ring "Bob," a 2-mo old ring; station 2 in ring "Al," a 6-mo old ring; station 6 in "Emerson," a relatively old ring; stations 7 and 8 in "Franklin," a middle-aged ring. The other stations were located in the Slope Water. For some comparisons data collected with the 1 m^2 MOCNESS on earlier cruises will be used; information about these tows (those noted in Table 2) is reported by Ortner et al. (1978). Station positions for the remaining tows are given in Table 1.

At the majority of stations day and night tows were taken with both the 1 m^2 and 10 m^2 MOCNESSes. The 1 m^2 net was equipped with nine nets of 333 μm nylon mesh netting dyed dark blue and was fished obliquely so that eight strata were sampled. Generally, the strata sampled were 1,000-850, 850-700, 700-550, 550-400, 400-300, 300-200, 200-100, 100-0 m; usually between 600 and 1,000 m^3 were filtered in each strata. Occasionally in the Slope Water when sharp hydrographic gradients were present, the sampling intervals were modified to bracket the physical discontinuities.

The 10 m^2 MOCNESS is a scaled up version of the 1 m^2 net system described by Wiebe et al. (1976). On the tows reported here, it was equipped with five nets of 3 mm nylon mesh white netting. This net system was fished obliquely with four of the five nets sampling 250 m intervals from 1,000 to the surface. Each net filtered between 13,000 and 43,000 m^3. As with the 1 m^2 MOCNESS, the first net is fished while lowering the system to the maximum depth of the tow to provide uniform drag and to prevent kiting of the system at the start of the stratified oblique haul. Neither system has a bridle in front of the nets.

The nets of both systems are opened and closed with commands sent via conducting cable from a surface deck unit. For both systems on *Knorr* 65, we used an underwater unit which measures and telemeters to the surface depth temperature, conductivity, angle of the net system from the vertical, flow past the net, and information regarding the electrical and mechanical function of the opening/closing mechanism. The trans-

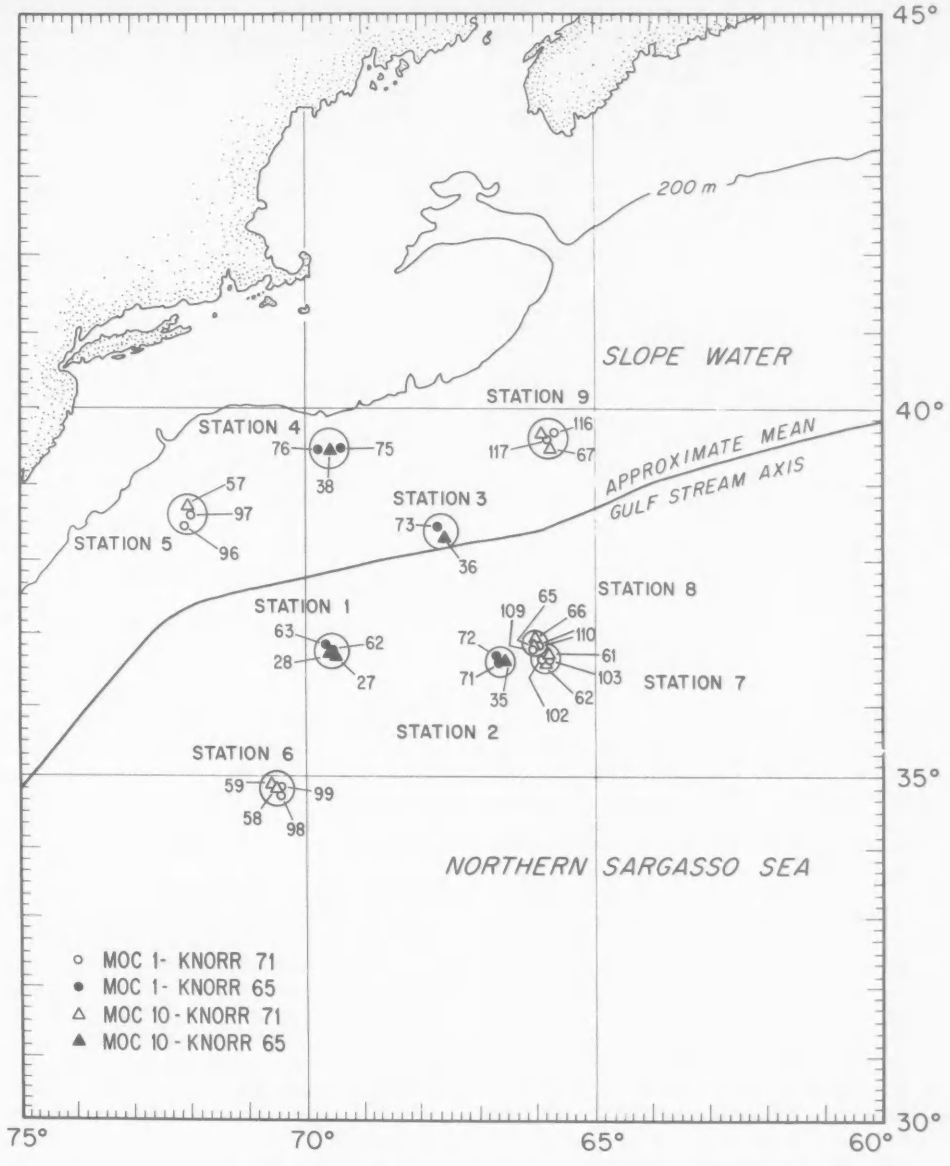

FIGURE 1.—Position of the 1 m² and 10 m² MOCNESS tows within each of the nine station areas (indicated by large open circles). Small solid triangles and circles are night tows; open ones are for day tows. Each tow listed in Table 1 is designated by its tow number.

TABLE 1.—Summary of tow statistical information for the 1 m^2 and 10 m^2 MOCNESS (MOC-1, MOC-10) tows taken in 1977 at the nine station locations illustrated in Figure 1. D = Day; N = Night.

Cruise no.	Station no.	MOC 1	Longitude W	Latitude N	Time of tow	MOC 10	Longitude W	Latitude N	Time of tow	Date of tow	MOC 1/MOC 10 10° isotherm depth (m)
Knorr 65	1	62 D	69°30.1' 69°30.8'	36°43.2' 36°47.8'	1019- 1228	27 D	69°30.0' 69°25.9'	36°46.5' 36°38.6'	1352- 1744	4/17	300/330
		63 N	69°33.0' 69°34.8'	36°49.0' 36°53.2'	0115- 0335	28 N	69°30.0' 69°27.2'	36°41.1' 36°49.0'	2055- 0030	4/17-18	296/270
	2	72 D	66°39.0' 66°38.8'	36°38.0' 36°35.6'	0910- 1128	35 D	66°36.9' 66°34.4'	36°35.6' 36°31.3'	1303- 1650	4/24	717/690
		71 N	66°39.6' 66°39.0'	36°30.5' 36°36.2'	2100- 2322					4/23	
	3	73 D	67°42.4' 67°37.5'	38°19.3' 38°21.3'	0955- 1128	36 D	67°37.0' 67°37.4'	38°21.3' 38°11.7'	1248- 1639	4/28	234/290
	4	76 D	69°41.3' 69°38.0'	39°24.0' 39°28.0'	0705- 0913					4/30	
		75 N	69°26.6' 69°31.9'	39°28.5' 39°25.1'	2107- 2314	38 N	69°31.0' 69°43.0'	39°24.6' 39°21.1'	2345- 0345	4/29-30	200/255
Knorr 71	5	96 D	72°03.0' 72°00.0'	38°25.9' 38°29.9'	0930- 1204					10/23	
		97 N	71°54.5' 71°52.1'	38°36.8' 38°40.6'	2201- 0015	57 N	71°54.1' 71°51.0'	38°39.9' 38°47.0'	0052- 0050	10/23-24	190/190
	6	98 N	70°20.2' 70°21.5'	34°46.5' 34°50.2'	2150- 0005	58 N	70°21.9' 70°16.0'	34°50.8' 34°52.0'	0201- 0501	10/28-29	545/550
	7	102 D	65°52.1' 65°47.0'	36°40.1' 36°42.3'	0471- 1104	61 D	65°46.9' 65°40.0'	36°43.0' 36°46.0'	1345- 1652	11/3	309/340
		103 N	65°53.5' 65°47.9'	36°40.0' 36°42.5'	2243- 0059	62 N	65°48.9' 65°40.0'	36°42.2' 36°48.0'	0123- 0502	11/3-4	360/330
	8	109 D	66°00.0' 66°00.8'	36°44.1' 36°49.1'	0910- 1138	65 D	65°58.3' 65°46.0'	36°49.0' 36°52.0'	1232- 1646	11/6	310/375
		110 N	65°57.8' 65°59.5'	36°49.8' 36°55.1'	1901- 2123	66 N	65°58.8' 66°10.0'	36°56.0' 37°05.0'	2140- 0213	11/6-7	278-290
	9	117 D	65°51.1' 65°51.2'	39°32.9' 39°38.8'	1117- 1359	67 D	65°42.1' 65°48.0'	39°26.0' 39°33.0'	1308- 1628	11/15	200/230
		116 N	65°47.0' 65°45.6'	39°35.0' 39°40.6'	1933- 2156	68 N	65°49.0' 65°51.0'	39°36.8' 39°35.0'	0026- 0500	11/15-16	232/205

mitted data were recorded on magnetic tape. They were also processed by a shipboard computer (Hewlett-Packard[4] 2100) and plots of depth versus temperature and salinity were produced. On *Knorr* 71, the 10 m^2 net was deployed with a simplified electronics package which did not have a conductivity sensor and which transmitted data at a slower rate. For this latter system, plots of depth versus temperature and angle of the net were made with a Hewlett-Packard X, Y, Y recorder. During all of these tows, net speed, as indicated by the flowmeter, was closely monitored and adjustments to the ship speed and/or winch speed were made to keep the net moving ahead at 2±0.5 kn (3.71±93 km/h). All samples were preserved in 5-10% Formalin buffered to pH 8.0 with sodium borate.

For 162 of the 190 samples resulting from the tows listed in Table 1, we sorted and counted the entire sample for adult and adolescent (without adult sexual characteristics) *N. megalops*. Very large catches were split with a Folsom plankton splitter (McEwen et al. 1954) and between one-half and one thirty-second of the sample was counted. Wet weights were determined either on all or a sizable fraction of the sorted individuals. Battered or disfigured individuals were excluded from this analysis. Individuals were blotted on absorbent paper and then weighed to ±0.1 mg on a Cahn model 7500 digital top-loader millibalance. Total body length (tip of rostrum to tip of telson) was determined on a small subset of individuals from both the *Knorr* 65 and 71 collections in order to establish a relationship between wet weight and length (Fig. 2) for subsequent calculations of potential escape velocity based on body length. The geometric mean regression equation (Ricker 1973) which was fit to these data is similar to those presented by Mauchline (1967) for a variety of euphausiid species.

In some comparisons of the sampling capabilities of the two MOCNESSes and in the application of Barkley's (1972) avoidance theory, we have used the average numbers per 1,000 m^3 for

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—The ratio (Night/Day) of night 1 m^2 and 10 m^2 MOCNESS catch of *Nematoscelis megalops* (no./m^2) divided by the paired day catch at stations in the Slope Water and cold core rings and the depth where the cumulated frequency of occurrence equals 50% in the night tow. Information about the tows taken on *Chain* 125 and *Knorr* 53 is given in Ortner et al. (1978).

Tow and cruise	Station or area	MOCNESS tow no. (night/day)	Night/Day[1]	Depth of 50% (m)
1 m^2 MOCNESS				
Knorr 65	Station 1	63/62	5.6	82
	Station 2	71/72	33.0	80
	Station 4	75/76	1.5	340
Knorr 71	Station 5	97/96	5.9	345
	Station 6	98/99	1.7	500
	Station 7	103/102	29.0	370
	Station 8	110/109	1.3	325
	Station 9	116/117	33.0	150
Chain 125	Slope Water	[1]20/21	63.4	220
	Slope Water	[1]19/18	10.9	260
	Ring "D"	[1]5/8	([2])	300
Knorr 53	Slope Water	35/37	48.9	280
	Slope Water	41/42	.57	380
	Slope Water	39/40	([2])	450
	Ring "D"	[1]29/27	2.7	650
	Ring "D"	[1]33/31	6.4	450
Knorr 62	Slope Water	57/58	1.5	245
	Ring "A!"	45/47	2.6	505
10 m^2 MOCNESS				
Knorr 65	Station 1	28/27	3.67	130
Knorr 71	Station 6	58/59	2.66	700
	Station 7	62/61	0.68 (1.47)	375
	Station 8	66/65	0.84 (1.19)	370
	Station 9	68/67	2.93	180

[1]Vertical distribution of *N. megalops* on these tows illustrated in figure 5 of Wiebe and Boyd (1978).
[2]None present in day collection.

the water column. These values were obtained by combining the stratified oblique hauls to form a composite tow. Note that because the water column sampled is 1,000 m, the integrated number per 1,000 m^3 for the column is identical to numbers per square meter.

RESULTS

Analysis of 1 m^2 and 10 m^2 MOCNESS Observations

The vertical distribution of *N. megalops* at stations where pairs of 1 m^2 and 10 m^2 MOCNESS tows were taken (Fig. 3) illustrates the large variations in depth distribution that can occur in the different hydrographic regimes and at different times of year. As previously described by Wiebe and Boyd (1978), this species generally has its center of distribution above 300 m in Slope Water. Exceptions in Slope Water are associated with the presence of warm core rings. In young cold core rings such as "Bob," the center of distribution is also shallow. In most of the older rings we have sampled, the distribution of *N. megalops* deepens as is evident in "Franklin" and "Emerson" (see also figure 5 in Wiebe and Boyde 1978).

Very close agreement between the two net systems in the shape of the vertical distribution is found, especially at night (Fig. 3). The night 1 m^2 and 10 m^2 MOCNESS tows also show significant agreement in the integrated numbers caught per square meter ($r = 0.99$; $P<0.05$). In contrast, the paired day tow data are considerably more variable and do not show significant agreement in integrated numbers per square meter ($r = 0.13$; $P>0.05$).

Clearest evidence for differential day/night net avoidance by *N. megalops* is found in the catch data obtained by the 1 m^2 MOCNESS (Fig. 3). Without exception, for each of the eight day/night pairs of tows taken on *Knorr* 65 and *Knorr* 71, the day estimate of numbers per square

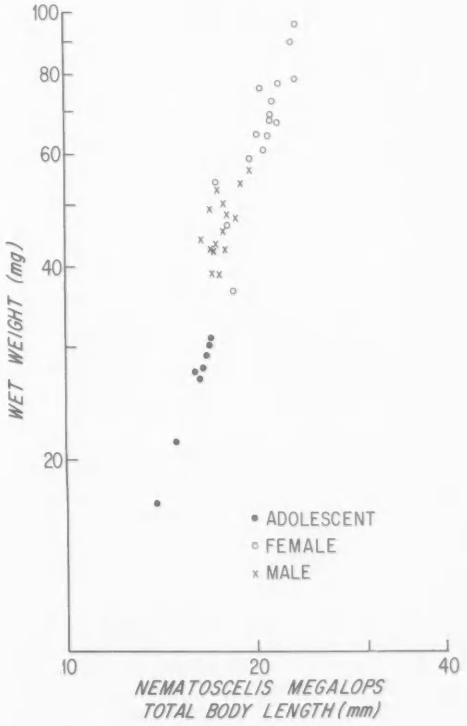

FIGURE 2.—Relationship between total body length, carapace length, and wet weight of *Nematoscelis megalops*.

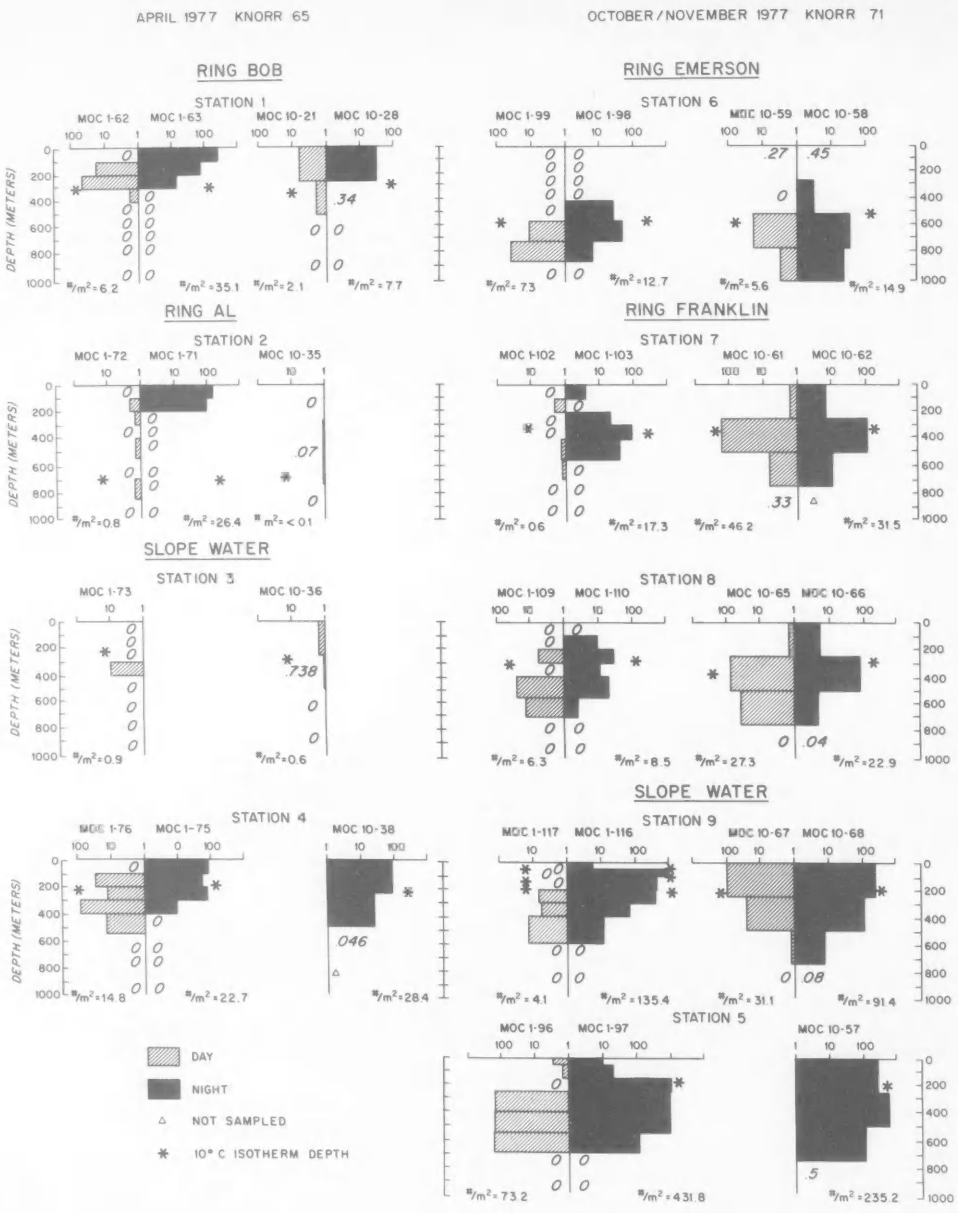

FIGURE 3.—Vertical distribution of *Nematoscelis megalops* in the Slope Water and in variously aged cold core rings based on collections made with the 1 m^2 and 10 m^2 MOCNESSes on two cruises taken 6 mo apart. Night samples are blacked; day samples are crosshatched.

meter for the water column is less than the corresponding night catch. In every case, sampling extended below the maximum depth of occurrence of the population and there is no evidence that any individuals of the population migrated vertically out of the depth zone sampled during the day. Therefore, it is highly significant that all of the day values were less than the respective night ones ($P<0.005$). This result gains importance if we also consider 10 other day/night pairs of 1 m^2 MOCNESS tows in which *N. megalops* was collected on previous cruises (*Chain* 125, *Knorr* 53, *Knorr* 62). For nine of these pairs, moderately to dramatically higher catches in the night tow were obtained (Table 2). The single exception to this pattern was a pair of Slope Water tows taken near the continental shelf in the wake region of a warm core ring (tows 41, 42). But these two tows were displaced in space by several miles, and the night tow was taken nearer the warm core ring where a lower catch might have been expected.

Of the 18 day/night pairs of 1 m^2 MOCNESS tows, 17 yield higher density estimates at night. Patchiness in the distribution of *N. megalops* contributed to variability to these estimates but as an unbiased variance component, it does not affect our expectation that one-half of the day and one-half of the night tows in day/night pairs should be the larger. Thus it is unlikely that patchiness of this species is responsible for the significantly higher night catches that we have observed ($P<0.001$). We know of no other explanation than avoidance to explain this result.

There are only five pairs of 10 m^2 MOCNESS observations of the vertical distribution of *N. megalops*. For two of these, the integrated day catch is larger than the corresponding night catch and, therefore, night catches are not significantly larger than day catches ($P>0.05$). This result either means that there is no day/night differential avoidance of the 10 m^2 net or that in the face of other sources of error such as patchiness, we have too few day/night pairs of observations to observe the avoidance effect. If avoidance were affecting only the smaller net then at least we would expect that the 1 m^2 net day catches per unit volume would be consistently smaller than the corresponding 10 m^2 net day catches. We might also expect that night catches with the 1 m^2 net would be smaller than the 10 m^2 net. Neither comparison yields a significant result ($P>0.05$; day MOCNESS 1 tows greater than day MOCNESS 10 tows in four out of seven comparisons; night MOCNESS 1 tows greater than night MOCNESS 10 tows in three out of seven comparisons). Thus within the limits of error, by day or by night both net systems provide comparable estimates of the number of *N. megalops* living in the water column at a given station.

It is possible that the lack of differences in the catching rates between the two nets is due to the different mesh sizes. Small individuals might have been caught more efficiently by the 1 m^2 net while larger individuals could have avoided this net better and conversely for the 10 m^2 net except that small individuals would have been lost due to escapement through the mesh. The size-frequency data in Figures 4 and 5 do not support this possibility. While there is considerable variability between net tow pairs, in terms of absolute abundance, neither net system systematically catches large or small individual *N. megalops* in the size range counted better than the other. A similar observation can be made if comparisons are made on the relative abundances in a given size class (Fig. 6).

There is one other potentially significant trend in the data that is important to note. The magnitude of the day/night avoidance does not appear to be uniform with depth. For the 1 m^2 MOCNESS, largest differences between paired night and day catches where both are positive occur when the center of distribution of *N. megalops* is above 300-400 m and minimum differences occur at or below these depths (Table 2). Linear regression of the ratio of night to day catch (N/D) versus depth of the center of the distribution at night (50% of occurrence with depth) is significant at $P = 0.1$. There is a similar pattern in the 10 m^2 MOCNESS tows, although as mentioned above, the day/night differences in catching rates are considerably smaller.

In summary, there is clear evidence for differential day/night avoidance of the 1 m^2 MOCNESS. Furthermore, there are no significant differences in the size range of adolescent or adult *N. megalops* caught by the 1 m^2 or 10 m^2 MOCNESS systems nor in either system's estimates of its abundance in the water column at a given station when day or night pairs are compared. Although differences between pairs of day/night catches for the 10 m^2 MOCNESS are statistically not significant, the entire data set when considered as a whole strongly suggests that *N. megalops* is also avoiding the 10 m^2 net, albeit to a lesser extent.

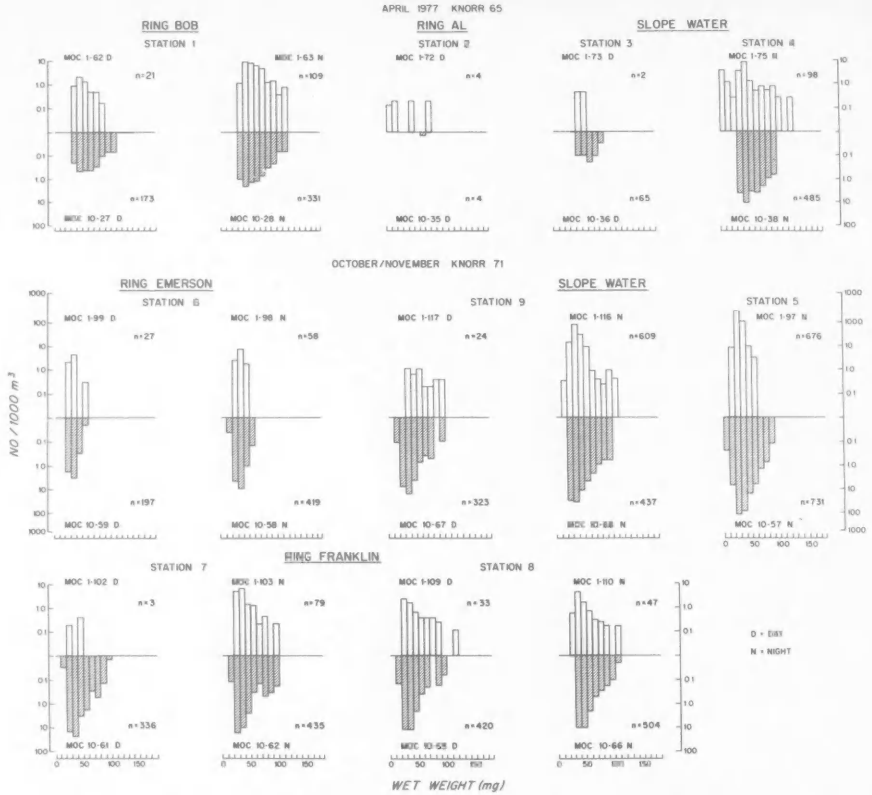

FIGURE 4.—Comparison of the composite size-frequency distribution (expressed as No./1,000 m^3 for a given wet weight interval) of *Nematoscelis megalops* caught by the MOCNESS 1 (shaded) and the MOCNESS 10 (crosshatched) for tows taken on the same day or night. n = the number of individuals used to construct the histogram.

Application of Barkley Avoidance Theory

Since it is likely that *N. megalops* avoids both net systems, it must detect the approach of either net at some distance in front of the net, resulting in a response which permits a certain percentage of the population to avoid capture. Determination of the avoidance percentage and reaction distance requires an indirect approach, since no other means are available. The theoretical framework on the process of net avoidance developed by Barkley (1964, 1972) provides a means for estimating these parameters according to a quantitative theoretical model. Barkley (1972) formulated the problem in the following way:

$$\text{Catch} = (\text{volume sampled}) \times (\text{no. of organisms unit volume}) \times (\text{probability of capture}) - (\text{losses}) \quad (1)$$

"Losses" refers to individuals which are enclosed by the net but escape through the net meshes. For the size range of individuals which constitute our "catch," the "losses" term is essentially zero. Since the volume of water sampled has been rather carefully measured, the "probability of capture" (Pc) is of greatest concern. Pc is related to the mean reaction distance (x_0), the radius of the net mouth (R), the net's speed (U), and the organism's mean escape speed (u_e) by the equa-

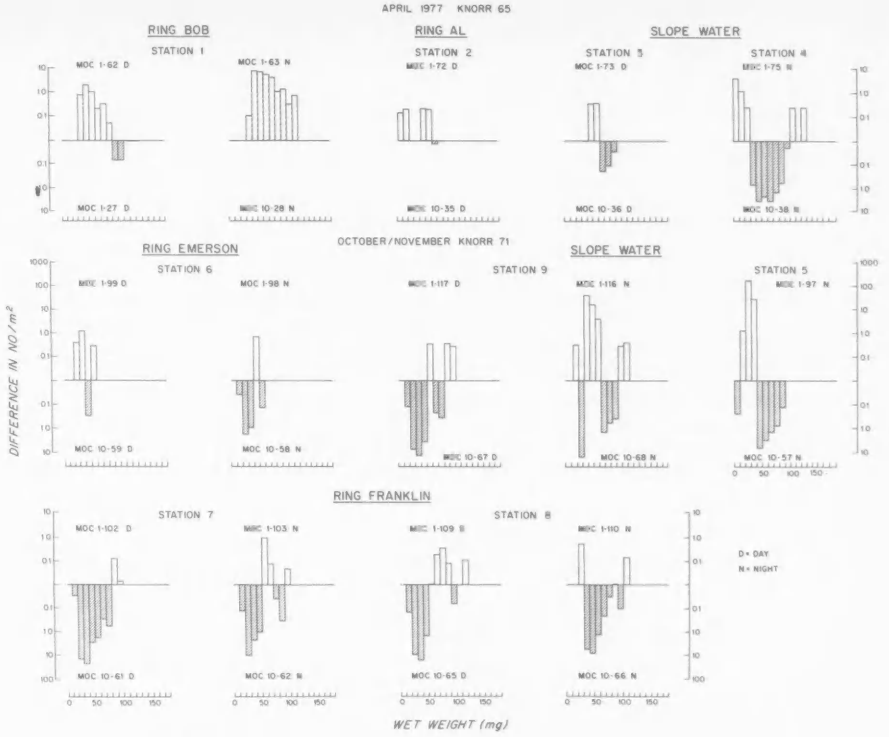

FIGURE 5.—Comparison of the difference between paired MOCNESS 1 and MOCNESS 10 catches in No./1,000 m³ for a given wet weight interval. For shaded columns above the line, the MOCNESS 1 catch is greater than the MOCNESS 10 catch and vice versa for crosshatched columns below the line.

tion derived by Barkley (1972, equation 6) wherein:

$$Pc = \left(1 - \frac{x_0\, u_e}{R(U^2 - u_e^2)^{1/2}}\right)^2. \qquad (2)$$

This expression assumes that as the net moves forward through the water, an individual senses the oncoming net and at a distance x_0 in front of the net begins a swimming response in a direction away from the net which is optimal for avoidance. Thus, this equation provides an estimate of the minimum probability of capture.

As a first step in applying these equations to our data, we may recall that for both the paired night tows and the paired day tows differences between the two net systems were not significant, i.e.,

$$\frac{10\ \text{m}^2\ \text{MOCNESS catch}}{\text{volume sampled}} \cong \frac{1\ \text{m}^2\ \text{MOCNESS catch}}{\text{volume sampled}}.$$

If we assume that the number of organisms per unit volume was a constant during the time each pair of tows was taken, then:

$$10\ \text{m}^2\ \text{MOCNESS}\ P_e = 1\ \text{m}^2\ \text{MOCNESS}\ P_e$$

and

$$\left(1 - \frac{x_{10} u_e}{150(100^2 - u_e^2)^{1/2}}\right)^2 = \left(1 - \frac{x_1 u_e}{50(100^2 - u_e^2)^{1/2}}\right)^2$$

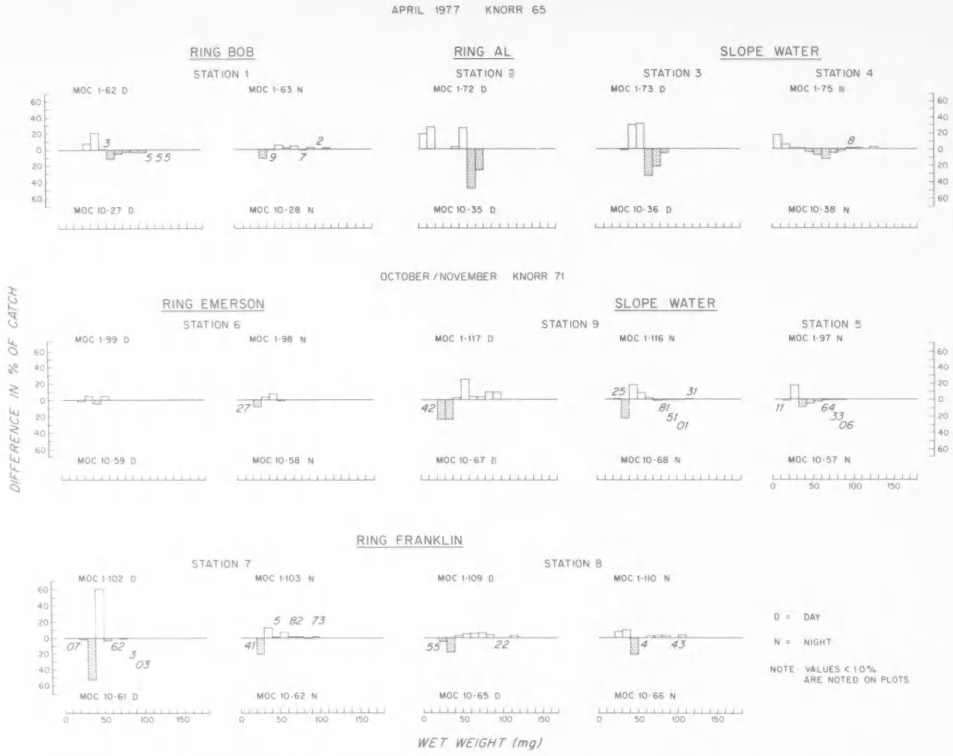

FIGURE 6.—Comparison of the difference between paired MOCNESS 1 and MOCNESS 10 tows in the percent of the catch in a given wet weight interval.

where x_{10} and x_1 refer to the reaction distance for the 10 m^2 and 1 m^2 net systems, where we have approximated the radius of the large net as 150 cm and the small net as 50 cm, and where both nets were towed at approximately 100 cm/s. We are also assuming that the mean swimming speed of the individuals (u_e) is the same for both nets. Solving for the ratio of the reaction distances we find:

$$\frac{x_{10}}{x_1} = 3.0.$$

That is, in order for the two net systems to provide numbers of *N. megalops* per volume filtered which are approximately the same, the reaction distance for the 10 m^2 MOCNESS must be three times greater than for the 1 m^2 MOCNESS.

Since we do not know the absolute abundance of *N. megalops* independent of our net tow estimates for any sampling period, we cannot directly estimate the absolute magnitude of the reaction distance or the minimum probability of capture for either net. It is possible to derive those estimates by a method described by Barkley (1972:808) which involves making a best fit of theoretically derived curves which relate P_c, u_e/U, and X_0/R to observations of u_e/U and the catch/volume filtered for each size class of individuals caught by the nets. In order to make these comparisons, we must have an estimate of the mean escape velocity of an individual (u_e) in a given size class, and ultimately we must make some assumption about population structure, i.e., abundance versus size class of the population sampled.

To make estimates of u_e, we have followed Barkley (1972) and used generalized swimming speed-body length relationships because there is no direct information about u_e for *N. megalops*. However, as discussed below, inconsistencies between model expectations and the field data develop when this assumption is applied. Our basic size-frequency data are in units of wet weight. However, as noted under "Methods," a subset of individuals of *N. megalops* from MOCNESS 10 tows were used to establish the relationship between wet weight and body length (Fig. 2). Mean body wet weight of individuals in each size class was converted to body length (L) and then to relative escape speeds (u_e/U) assuming initially that $u_e = 10\ L$. This assumption is supported by work of Kils (1979) and Semenov (1969). Relative escape speeds were plotted versus the catch/1,000 m^3 in each size class on semilog graph paper scaled so that each plot could overlay a reproduction of the upper panel of Barkley's figure 3 (1972:805). These plots were adjusted vertically to obtain a "best" fit with the x_0/R curves such that a maximum number of points fell between any two of the x_0/R curves (Fig. 7). This produces an estimate of x_0 if it is assumed that the shape of the size-frequency distribution is entirely produced by improvement of avoidance capability with increasing size.

Estimates of reaction distance (x_0) for each net system (Table 3) are between 1.7 and 2.3 for the 1 m^2 MOCNESS and between 4.9 and 6.6 m for the 10 m^2 MOCNESS. No significant differences between night x_0's and day x_0's for either net system are observable. Our initial conclusion was that this was an unreasonable result since intuitively one would expect an increased night catch to be related to reduced nighttime x_0 values

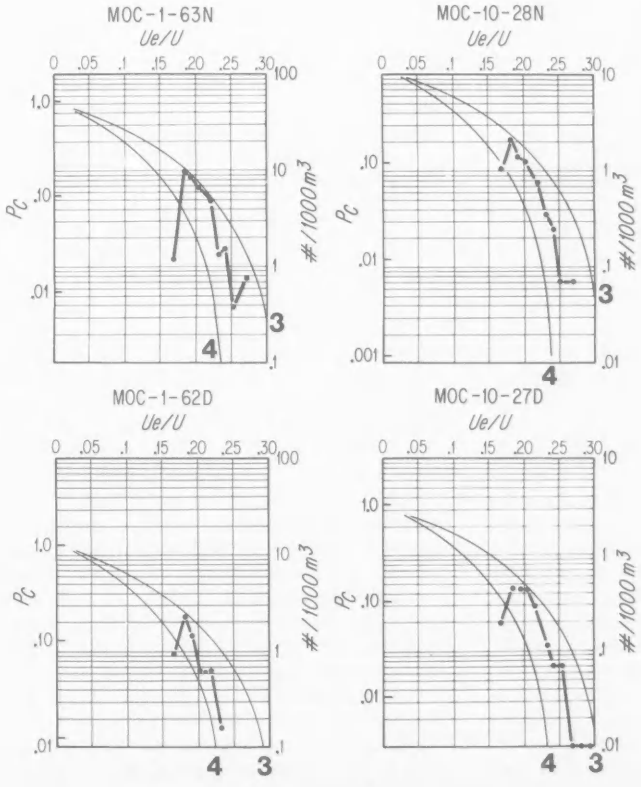

FIGURE 7.—Examples of relative escape speed of *Nematoscelis megalops* individuals versus the catch per 1,000 m^3. Superimposed on this plot are the theoretically derived curves of x_0/R as a function P_c and u_e/U adjusted to give a "best" fit of the observed points.

if individual escape speeds remained constant. However, further analysis reveals that the difference in x_0 for a given day/night catch differential could be a function of the relationship between the observed night catch and the true water column abundance. This is clearly evident if we express the ratio of the day catch per volume sampled (DC) and night catch per volume sampled (NC) in terms of real abundance (A) and percent capture as expressed in Equation (2):

$$\frac{DC}{NC} = A\left(1 - \frac{x_D}{R\sqrt{\frac{U^2}{u_D^2} - 1}}\right)^2 \Bigg/ A\left(1 - \frac{x_N}{R\sqrt{\frac{U^2}{u_N^2} - 1}}\right)^2. \quad (3)$$

If we assume that the daytime escape speed, u_D, is equal to the nighttime speed, u_N, and solve for the ratio of the daytime reaction distance, x_D, to the nighttime reaction distance, x_N, we have:

$$x_D/x_N = \left(\frac{DC}{NC}\right)^{\frac{1}{2}} + \frac{1}{1 - \left(\frac{NC}{A}\right)^{\frac{1}{2}}} - \frac{\left(\frac{DC}{NC}\right)^{\frac{1}{2}}}{1 - \left(\frac{NC}{A}\right)^{\frac{1}{2}}}. \quad (4)$$

We have evaluated this equation assuming a true abundance of 100 individuals per volume, nighttime catches of 99, 90, 10, 1, and 0.1 individuals per volume, and daytime catches of 50, 10 and 1% of the nighttime catch. The ratios of x_D/x_N, plotted as a function of the ratio of NC/A Fig. 8a), shows that only very small differences in reaction distance between day and night are required to explain large day/night catch differentials when the night catch is 10% or less of the true water column abundance. The fact that we see no significant difference in day/night reaction distances suggests our nighttime catches also could be affected strongly by avoidance, and that even at night we have significantly underestimated the numbers of *N. megalops* in the water column.

It could be argued that the day/night catch differential is due to differences in escape speed of the individuals rather than a change in their reaction distance. To explore this we have also solved Equation (3) for the ratio of day escape speed, u_D, to night escape speed, u_N, after assuming $x_D = x_N$.

$$u_D/u_N = \left[\frac{\left[\left(\frac{DC}{A}\right)^{\frac{1}{2}} - 1\right]^2 * \left[\left(\frac{NC}{A}\right)^{\frac{1}{2}} - 1\right]^2 + \left[\left(\frac{DC}{A}\right)^{\frac{1}{2}} - 1\right]^2 * \left[\frac{X_n}{R}\right]^2}{\left[\left(\frac{DC}{A}\right)^{\frac{1}{2}} - 1\right]^2 * \left[\left(\frac{NC}{A}\right)^{\frac{1}{2}} - 1\right]^2 \left[\left(\frac{NC}{A}\right)^{\frac{1}{2}} - 1\right]^2 * \left[\frac{X_n}{R}\right]^2}\right]^{\frac{1}{2}}. \quad (5)$$

Note that the ratio of day/night escape speeds is a function of x_N and R as well as DC, NC, and A. The escape speed and radius of net were not in Equation (4) for the ratio of day/night reaction distances. We have evaluated this ratio using the same values noted above. With these results (Fig. 8b), we reach a conclusion similar to that for reaction distance, namely, if reaction distance remains constant between day and night, then small differences in escape speed can explain the day/night catch differential when the night catch is 10% or less of the true abundance.

There is, however, an entirely different explanation which may account for this outcome in application of Barkley avoidance theory to our data. In fitting these data to Barkley's plots of percent capture versus the ratio of x_0/R, two assumptions were required: 1) that all changes in size frequency are due to avoidance and 2) that swimming speed is a function of body size. The second assumption can be examined if one has day/night pairs of tows taken at the same station location with the same size of net. With swimming speed a function of size, Barkley's model

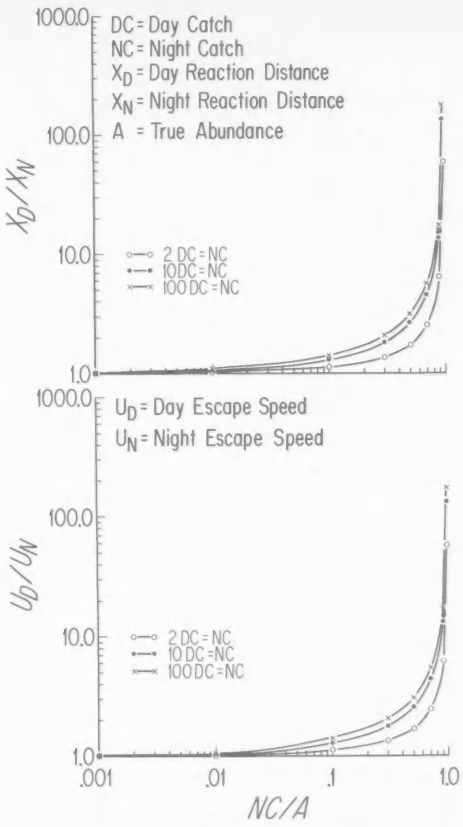

FIGURE 8.—Relationships between the ratio of night catch to true abundance (NC/A) and a) the ratio of day and night reaction distances (x_D/x_N), and b) the ratio of day and night escape speeds (u_D/u_N).

TABLE 3.—*Nematoscelis megalops* reaction distances (x_0) for the 1 m² and 10 m² MOCNESS nets derived from the plots like those in Figure 7.

Station	Cruise	Tow	Day/Night	x_0/R	x_0
1	*Knorr* 65	M-1-62	D	3.4	1.7
		M-10-27		3.3	5.0
		M-1-63	N	3.4	1.7
		M-10-28		3.4	5.0
3	*Knorr* 65	M-1-73	D	3.4	1.7
		M-10-36		(1)	(1)
4	*Knorr* 65	M-1-75	N	(1)	(1)
		M-10-38		3.4	5.0
5	*Knorr* 71	M-1-97	N	4.5	2.3
		M-10-57		4.4	6.6
6	*Knorr* 71	M-1-99	D	4.5	2.3
		M-10-59		4.4	6.5
		M-1-98	N	4.5	2.3
		M-10-58		4.4	6.6
7	*Knorr* 71	M-1-102	D	4.4	2.2
		M-10-61		(1)	(1)
		M-1-103	N	4.4	2.2
		M-10-62		4.4	6.6
8	*Knorr* 71	M-1-109	D	3.5	1.8
		M-10-65		4.4	6.6
		M-1-110	N	4.3	2.2
		M-10-66		4.3	6.4
9	*Knorr* 71	M-1-117	D	3.5	1.8
		M-10-67		4.4	6.6
		M-1-116	N	4.4	2.2
		M-10-68		4.3	6.5

[1]Not sufficient points to derive an estimate; Station 2 omitted for this reason.

TABLE 4.—The ratio of night catch to day catch as a function of individual swimming speed (u_e) as predicted by Barkley's avoidance model (inverse of Equation 3). u_e is assumed to be a function of body size as described in the text.

Body wet weight (mg)	u_e (cm/s)	Night catch[1]	Day catch[1]	Ratio
20	15.08	0.294	0.217	1.35
30	16.32	0.253	0.177	1.43
40	17.56	0.216	0.141	1.53
50	18.80	0.181	0.108	1.66
60	20.04	0.149	0.080	1.84
70	21.28	0.120	0.056	2.12
80	22.52	0.093	0.036	2.57
90	23.76	0.070	0.020	3.42
100	25.00	0.050	0.009	5.47
110	26.24	0.033	0.002	14.57
120	27.48	0.022	0.000	—

[1]Catch units are proportion of individuals present per unit volume.

predicts that the ratio of the number of individuals caught per size class at night (NC) to those caught during the day (DC) will increase with increasing individual size (the inverse of Equation 3).

This relationship is illustrated in Table 4 where u_N and u_D are assumed to be equal and 10 body lengths/s, $x_D = 175$ cm, $x_N = 150$ cm, $R = 50$ cm, and $U = 100$ cm/s. This ratio increases dramatically with individual size until at the largest size, the model predicts all individuals avoid capture. No such pattern emerges if we compute the ratio NC/DC for each size class in our paired day/night MOCNESS 1 or MOCNESS 10 tows (Table 5). Thus, the assumption of increasing swimming speed with increasing size does not appear to be valid, i.e., for the size range of individuals used in this study, avoidance swimming speeds are essentially the same. One implication of this finding is that the size-frequency distributions evident in the field data may not be seriously biased by the avoidance although the estimates of average density clearly are.

TABLE 5.—Ratios of night to day catches (number per square meter) of *Nematoscelis megalops* as a function of size for stations where both the MOCNESS 1 and the MOCNESS 10 were taken. ∞ indicates only the night tow caught individuals in the given size class; 0 indicates the opposite patterns.

Body wet weight (mg)	MOCNESS 1—tow no.:					MOCNESS 10—tow no.:				
	117/116	62/63	99/98	102/103	109/110	27/28	59/58	61/62	65/66	67/68
10	∞	—	—	—	—	—	∞	4.4	0	0
20	∞	—	1.2	33.3	0.3	—	2.4	1.1	<0.1	4.0
30	66.6	1.3	1.7	∞	2.6	5.9	2.6	0.4	0.8	2.2
40	45.5	4.0	∞	3.7	2.6	4.8	3.6	0.8	4.8	2.9
50	7.9	5.6	0	∞	1.9	3.6	7.7	0.2	5.6	5.9
60	4.6	1.1	—	∞	0.8	3.2	—	0.5	2.8	5.9
70	2.1	7.7	—	∞	0.7	2.6	—	0.9	∞	1.8
80	0.6	7.7	—	—	0.7	2.9	—	2.5	1.0	∞
90	2.4	∞	—	∞	—	3.5	—	12.5	1.7	6.3
100	∞	∞	—	—	∞	1.0	—	—	∞	—
110	—	∞	—	—	0	7.1	—	—	—	—
120	—	—	—	—	—	0	—	—	—	—
130	—	—	—	—	—	0	—	—	—	—

DISCUSSION

From this application of the Barkley avoidance theory, it appears that estimates of *N. megalops* water column abundance could be substantially underestimated by both nets, even at night. Minimum probabilities of capture derived from best fits to model expectations are 0.1 or less for night catches and 0.01 or less for day catches. However, the fact that we cannot demonstrate a dependence of the ratio of night to day catches on the size of individuals caught strongly suggests the size dependent swimming speed assumption required to apply the model is not valid for this species, a result which is apparently supported by Kils's (1979) data for *Euphausia superba* escape swimming (tail swimming). Being unable to make this assumption means that the field population size-frequency distribution which was observed is probably not materially affected by avoidance. Undeniably some fraction of the *N. megalops* population is avoiding the net systems, and the problem is serious enough to merit an effort to reduce this bias, i.e., to prevent the avoidance from taking place.

The usual strategies suggested to reduce net avoidance, increasing net speed or net size, have serious shortcomings in this case. Our evidence strongly implies that *N. megalops'* response to increased net size is to increase its reaction distance so that the catch rate remains relatively constant. Barkley (1972) reached the same conclusion in a comparison of 1 m diameter net and 3 m IKMT (Isaacs-Kidd midwater trawl) catching rates of the northern anchovy, *Engraulis mordax*. It is possible that by going to still larger nets (i.e., >10 m^2 mouth areas), a reduction in the bias could be effected. However, larger nets would be impractical, if not impossible, to handle on most oceanographic vessels.

As Barkley (1964) has demonstrated, increased net speed is not a feasible strategy for avoidance reduction since increasing the towing speed of a net requires a compensatory reduction in net size. The practical limits to increasing the tow speed are reached at 2 to 3 kn, because of unavoidably extreme wire angles and inordinate amounts of wire required to fish even at moderate depths (to 1,000 m). High speed tows generally result in damaged specimens, reducing their value in studies requiring taxonomic identification or in physiological and biochemical measurements. Finally, as speed of net is increased, the effects of escapement through the meshes is enhanced.

Another means of reducing avoidance, that of camouflaging the net to reduce an animal's ability to detect its presence and thereby reducing the avoidance reaction distance, has been discussed briefly by Clutter and Anraku (1968). There is evidence that it may be an effective strategy for species such as *N. megalops* (LeBrasseur and McAllister, unpublished data cited by Clutter and Anraku 1968). To use this approach, one must first know what kind of a signal the animal is using to detect the oncoming net. Camouflaging the net can be accomplished by reducing the signal until it becomes part of the background (omnidirectional noise). Alternatively, the noise level could be increased until the signal is no longer detectable.

Signals emanating from a net and towing cable include deformation of flow, near field (displacement dominant) or far field (pressure dominant) sound, and light (bioluminescence) (Clutter and Anraku 1968). The importance of

these different signals obviously depends upon the net structure and towing cable configuration and upon the ability of *N. megalops* to sense the various signals. Although there is no direct experimental information about *N. megalops*' sensory capabilities or about the signals being generated by MOCNESS, it seems clear that the primary avoidance stimulus involves day to night variations in light. *Nematoscelis megalops* must use vision to detect the net and can better avoid the net during the day than at night because during the day the net is better illuminated. A fundamental link between the amount of light present and the magnitude of the avoidance is provided by our observation that as individuals live deeper in the water column under substantially reduced daytime light levels, day/night differences in catch rates decline.

But if we accept the results gained by the application of Barkley's model which indicate substantial avoidance takes place at night in the absence of bright sunlight, then other factors must also be important. We propose that bioluminescence is the principal signal and that vision remains the principal means of detection.

Three lines of evidence support the importance of bioluminescence as an avoidance cue. First, in an experiment conducted in the early 1960's, Boden (1969) equipped an IKMT with light meters so that he could monitor the amount of light produced above, below, in front of, and inside the trawl as it was towed at night. Bioluminescent light above the trawl was less than below the trawl but both were considerably lower than that ahead of or in the net. Light within the net was so bright that it recorded off scale and individual flashes were often too numerous to be recorded as such. Light ahead of the net was also exceedingly bright. Boden (1969) speculated that the light ahead of the net was caused by organisms flashing either in response to the light within the net or to pressure or sound waves propagating forward from the net. Second, Neshyba's (1967) experiments with a submarine photometer and strobe light showed that mesopelagic and epipelagic organisms could be stimulated to produce significant amounts of bioluminescence (10^{-4} $\mu W/cm^2$) for a sustained period by proper strobe light flashing. In the absence of artificial flashing, he observed a much lower level of irregular flashing (10^{-8}-10^{-7} $\mu W/cm^2$) similar to that reported by Kampa and Boden (1956), Clarke and Backus (1964), and Boden et al. (1965). Third, it is known that the eyes of euphausiids and decapod shrimps living at midwater depths during the day (i.e., 200-600 m) are sensitive to light levels (10^{-7} to possibly 10^{-9} $\mu W/cm^2$, Clarke 1970) significantly lower than that produced as a result of bioluminescence.

These lines of evidence suggest that the light generated by organisms when they come in direct contact with the nets or encounter turbulence caused by the net is used by individuals ahead of the net to detect its presence and begin an avoidance response. It seems likely that the light ahead of the net observed by Boden (1969) was caused by the same kind of response mechanism described by Neshyba (1967), i.e., flashing in response to flashing.

The tactic of reducing the visual contrast between a net and the surrounding water was demonstrated by LeBrasseur and McAllister (unpublished data cited by Clutter and Anraku 1968) to reduce the avoidance error for euphausiids both day and night. However, if bioluminescence in and ahead of the net is an important cue as we suspect it to be, then a more active means of camouflaging the net is required.

It is known from recent evidence (Warner et al. 1979) that decapod crustacea living at the same depth as *N. megalops* are easily "blinded" by even moderate amounts of light. This suggests the possibility of equipping the mouth of a net with a "blinding" light system to be used to periodically illuminate a region ahead of the net with enough light to temporarily blind individuals in the net. With the light out, individuals so affected by the light pulse would be unable to see and, therefore, to respond to the much lower light generated by zooplankton being captured by the net. We postulate that individuals outside the zone of temporary blindness may respond by electing a startle response, but, because the volume illuminated would be so large, their movement would be random with respect to the volume to be filtered by the net. Clearly, considerably more research is required before this strategy could be considered feasible.

There are two precautionary notes that must be made. First, in spite of avoidance error, vertical distribution patterns obtained in sampling this species with MOCNESS at different times under different hydrographic regimes are replicable (Fig. 3). That is, although avoidance error is strongly affecting the numerical estimates, the shape of the vertical distributions seem much less affected. Thus, in spite of the avoidance, we believe we are obtaining valuable ecological in-

formation about this species. Second, for most species of euphausiids and many copepods, chaetognaths, and pteropods in our collections, we have no evidence that differential day/night avoidance is taking place. Therefore, for many ecological studies of oceanic zooplankton, nets still seem the most effective tool to use to quantitatively collect them.

ACKNOWLEDGMENTS

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LITERATURE CITED

BARKLEY, R. A.
1964. The theoretical effectiveness of towed-net samplers as related to sampler size and to swimming speed of organisms. J. Cons. 29:146-157.
1972. Selectivity of towed-net samplers. Fish. Bull., U.S. 70:799-820.

BODEN, B. P.
1969. Observations of bioluminescence on SOND 1965 cruise of R.R.S. 'Discovery'. J. Mar. Biol. Assoc. U.K. 49:669-682.

BODEN, B. P., E. M. KAMPA, AND J. M. SNODGRASS.
1965. Measurements of spontaneous bioluminescence in the sea. Nature (Lond.) 208:1078-1080.

BOYD, S. H., P. H. WIEBE, AND J. L. COX.
1978. Limits of *Nematoscelis megalops* in the Northwest Atlantic in relation to Gulf Stream cold core rings. II. Physiological and biochemical effects of expatriation. J. Mar. Res. 36:143-159.

BRINTON, E.
1967. Vertical migration and avoidance capability of euphasiids in the California Current. Limnol. Oceanogr. 12:451-483.

CLARKE, G. L.
1970. Light conditions in the sea in relation to the diurnal vertical migrations of animals. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 41-48. U.S. Gov. Print. Off., Wash., D.C.

CLARKE, G. L., AND R. H. BACKUS.
1964. Interrelations between the vertical migration of deep scattering layers, bioluminescence, and changes in daylight in the sea. Bull. Inst. Oceanogr. Monaco 64(1318), 36 p.

CLUTTER, R. I., AND M. ANRAKU.
1968. Avoidance of samplers. *In* Zooplankton sampling, p. 57-76. UNESCO Monogr. Oceanogr. Methodol. 2.

FLEMINGER, A., AND R. I. CLUTTER.
1965. Avoidance of towed nets by zooplankton. Limnol. Oceanogr. 10:96-104.

HAURY, L. R., J. A. MCGOWAN, AND P. H. WIEBE.
1978. Patterns and processes in the time-space scales of plankton distributions. *In* J. H. Steele (editor), Spatial pattern in plankton communities, p. 277-327. Plenum Press, N.Y.

ISAACS, J. D.
1965. Larval sardine and anchovy interrelationships. Calif. Coop. Oceanic Fish. Invest. Rep. 10:102-140.

KAMPA, E. M., AND B. P. BODEN.
1956. Light generation in a sonic-scattering layer. Deep-Sea Res. 4:73-92.

KILS, U.
1979. Swimming speed and escape capacity of Antarctic krill, *Euphausia superba*. Meeresforschung 27:264-266.

LAI, D. Y., AND P. L. RICHARDSON.
1977. Distribution and movement of Gulf Stream rings. J. Phys. Oceanogr. 7:670-683.

LAVAL, PH.
1974. Un modèle mathématique de l'évitement d'un filet à plancton, son application pratique, et sa vérification indirecte en recourant au parasitisme de l'amphipode hypéride *Vibilia armata* Bovallius. J. Exp. Mar. Biol. Ecol. 14:57-87.

MACKAS, D. L., AND C. M. BOYD.
1979. Spectral analysis of zooplankton spatial heterogeneity. Science (Wash., D.C.) 204:62-64.

MAUCHLINE, J.
1967. Volume and weight characteristics of species of Euphausiacea. Crustaceana 13:241-248.

MCEWEN, G. F., M. W. JOHNSON, AND TH. R. FOLSOM.
1954. A statistical analysis of the performance of the Folsom plankton sample splitter, based upon test observations. Arch. Meteorol. Geophys. Bioklimatol., Ser. A Meteorol. Geophys. 7:502-527.

MCGOWAN, J. A., AND V. J. FRAUNDORF.
1966. The relationship between size of net used and estimates of zooplankton diversity. Limnol. Oceanogr. 11: 456-469.

MURPHY, G. I., AND R. I. CLUTTER.
1972. Sampling anchovy larvae with a plankton purse seine. Fish. Bull., U.S. 70:789-798.

NESHYBA, S.
1967. Pulsed light stimulation of marine bioluminescence *in situ*. Limnol. Oceanogr. 12:222-235.

ORTNER, P. B., P. H. WIEBE, L. HAURY, AND S. BOYD.
1978. Variability in zooplankton biomass distribution in the northern Sargasso Sea: The contribution of Gulf Stream cold core rings. Fish. Bull., U.S. 76:323-334.

RICHARDSON, P. L.
1980. Gulf Stream ring trajectories. J. Phys. Oceanogr. 10:90-104.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.
SEMENOV, V. N.
1969. Observations of krill behaviour in an aquarium. Tr. VNIRO 66:235-239.
SMITH, P. E., R. C. COUNTS, AND R. I. CLUTTER.
1968. Changes in filtering efficiency of plankton nets due to clogging under tow. J. Cons. 32:232-248.
VANNUCCI, M.
1968. Loss of organisms through the meshes. *In* Zooplankton sampling, p. 77-86. UNESCO Monogr. Oceanogr. Methodol. 2.
WARNER, J. A., M. I. LATZ, AND J. F. CASE.
1979. Cryptic bioluminescence in a midwater shrimp. Science (Wash., D.C.) 203:1109-1110.
WIEBE, P. H.
1971. A computer model study of zooplankton patchiness and its effects on sampling error. Limnol. Oceanogr. 16:29-38.
WIEBE, P. H., AND S. BOYD.
1978. Limits of *Nematoscelis megalops* in the Northwestern Atlantic in relation to Gulf Stream cold core rings. Part I. Horizontal and vertical distributions. J. Mar. Res. 36:119-142.
WIEBE, P. H., K. H. BURT, S. H. BOYD, AND A. W. MORTON.
1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. J. Mar. Res. 34:313-326.
WIEBE, P. H., AND W. R. HOLLAND.
1968. Plankton patchiness: Effects on repeated net tows. Limnol. Oceanogr. 13:315-321.
WIEBE, P. H., G. D. GRICE, AND E. HOAGLAND.
1973. Acid-iron waste as a factor affecting the distribution and abundance of zooplankton in the New York Bight. II. Spatial variations in the field and implications for monitoring studies. Estaurine Coastal Mar. Sci. 1: 51-64.

AGE AND GROWTH OF A PLEURONECTID, *PAROPHRYS VETULUS*, DURING THE PELAGIC LARVAL PERIOD IN OREGON COASTAL WATERS

JOANNE LYCZKOWSKI LAROCHE, SALLY L. RICHARDSON,[1] AND ANDREW A. ROSENBERG[2]

ABSTRACT

The age of 331 field-collected English sole, *Parophrys vetulus*, larvae, 3.1-20.0 mm SL, was determined using daily otolith growth increments. Age in days from hatching was estimated by adding 5, the number of days prior to first increment formation in the laboratory, to the number of increments counted on sagittae. Number of otolith growth increments among larvae of known age in the laboratory ranged widely. Yet daily periodicity of increment formation in *P. vetulus* was inferred from the observations that even under poor growing conditions some larvae added one increment each day since first formation and that, unlike the remaining laboratory-reared larvae in which no pattern was evident, increment addition among larvae in the sea appeared to follow a stable and uniform pattern.

Gompertz and von Bertalanffy growth models fitted the resultant size-at-age data equally well; therefore, only the Gompertz model is presented. Larval growth rate decreased from 0.3 mm per day at 8-9 days of age to <0.1 mm per day between 73 and 74 days. The oldest specimen was 74 days old, but most of the larval and transforming specimens collected in plankton samples were <70 days old.

Previous estimates of age at length of larval *P. vetulus*, based on length-frequency modal progression analysis, overestimated the age of larvae >5.5 mm SL by 2-3 times and, correspondingly, the duration of pelagic life was overestimated, 18-20 weeks compared to 8-10 weeks based on otolith-estimated age.

Saccular otoliths grow by addition of layers of material differing in the relative amount of the protein, otolin, and calcium carbonate in the aragonite form (Degens et al. 1969; Pannella 1971). This results in growth units or increments composed of an inner light band and an outer dark band. Once the cycle of formation has been established for a species, otolith growth increments can be used to estimate a fish's age and as a record of its past growth. Daily periodicity of increment formation has been confirmed in numerous species by the number of first-order growth increments within annuli in fish over 1 yr of age (Pannella 1971, 1974), by inspection of otoliths from reared fish of known age (Brothers et al. 1976; Taubert and Coble 1977), or from fish maintained in the laboratory for a known period of time (Struhsaker and Uchiyama 1976). Bands of daily increments are often grouped into fortnightly and monthly growth patterns (Pannella 1974; Rosenberg 1980). Subdaily increments, which appear faint and indistinct, when compared to daily increments, have been found in some species (Taubert and Coble 1977; Brothers and McFarland in press).

The daily increment method of aging larval and juvenile fishes can be used in fishery research to document the timing and duration of spawning, development, and major life history stages and events. The singlemost important application is the accurate determination of growth rates during early life in the sea. This technique has been applied to relatively few species, however, and much remains to be learned about how growth may change during development and under varying environmental conditions. Once specific growth rates are available, age-dependent larval mortality rates can be estimated and used to improve estimates of spawning stock biomass and also, perhaps, provide insight into recruitment success.

This paper documents the existence of daily growth increments in laboratory-reared and field-caught larvae of an eastern North Pacific pleuronectid, the English sole, *Parophrys vetulus*. It provides the first accurate estimates of

[1]Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, MS 39564.
[2]Department of Oceanography, Dalhousie University, Halifax, N.S., Canada.

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age at length for larvae of this species and describes the growth of larvae collected in Oregon coastal waters during the 1977-78 spawning season. It is the first detailed study of larval growth of a pleuronectid throughout the pelagic period, and further, provides a basis for the documentation of growth during transformation to the adult form (Rosenberg and Laroche 1982) and of juveniles in nursery grounds off the Oregon coast (Rosenberg 1980).

METHODS

Spawning and Rearing Procedures

Ripe adult *P. vetulus* were collected during fall and winter 1978 with a 12 m otter trawl off the Oregon coast in the vicinity of Hecata Head, approximately lat. 44°10′N, long. 124°18′W, 68-77 m water depth. Eggs were artificially fertilized on shipboard (Bagenal and Braum 1971) and transported back to the laboratory in seawater-filled plastic bags.

In the laboratory, eggs were incubated and larvae reared at 12°-13°C and under a 14-h light, 10-h dark photoperiod in filtered seawater taken from the area where the adults were captured. Eggs held in 4 l glass jars hatched in 3-3½ d. The newly hatched larvae were transferred by pipette to new 4 l glass jars or 8 and 9 l plastic tubs in which a bloom of the green flagellate *Tetraselmis* sp. was maintained throughout the rearing period. Approximately every 2 d, one-fourth to one-third of the water in rearing containers was replaced. On day 4 after hatching, *Gymnodinium splendens*, a naked dinoflagellate, and *Brachionus plicatilis*, a rotifer, were introduced into the rearing containers. After 1-2 wk, *G. splendens* was no longer added because larvae did not appear to eat this organism. Prey concentrations were not measured but *B. plicatilis*, the primary food item, was maintained at high levels, i.e., rotifers were readily visible throughout rearing containers. *Artemia salina* nauplii and the harpacticoid copepod, *Tisbe* sp., provided secondary food sources.

One to ten larvae were preserved in ~80% ethanol each day after hatching for the first 35 d; subsequently, older larvae were preserved at irregular intervals. Larvae were reared from two separate spawnings, in early and late fall 1978, but since rearing conditions were identical, age and growth data from the two were combined.

Field and Laboratory Procedures

Parophrys vetulus larvae were collected in the field with 70 cm, 0.505 mm mesh bongo nets in bottom to surface stepped, oblique tows. Samples were taken approximately monthly from November 1977 to June 1978 in Yaquina Bay, Oreg., and 2-7 km offshore (lat. ~44°37′N; long. 124°05′W). Samples were drained and preserved in ~80% ethanol; within 12-18 h the samples were drained again and fresh preservative was added. With each plankton sample surface temperature, surface and bottom salinity were recorded and a bathythermograph cast was made.

In the laboratory all fish larvae were removed from plankton samples and stored in ~80% ethanol. Otoliths were removed from *P. vetulus* larvae within 6 mo of initial preservation because longer storage resulted in erosion or complete dissolution of the otoliths.

Prior to otolith removal *P. vetulus* larvae were placed in freshwater for ~1-2 min (somewhat longer for specimens >15 mm) to remove or dilute ethanol in the tissue. A larva was then placed in a drop of water on either a glass slide or large rectangular cover slip under a dissecting microscope fitted with polarizing filter and analyzer. Standard length (SL) was measured with an ocular micrometer to the nearest 0.1 mm and both sagittae were dissected out with fine probes at 25 × or 50 × magnification. The larva was removed from the slide or slip and the otoliths were left to dry concave side up. Sagittae were then permanently mounted under a cover slip with Pro-Texx,[3] a clear mounting medium. Rectangular cover slip mounts, which were thought to improve the optical properties of the preparation, were taped for support to a thin piece of brass for viewing under the microscope.

Otolith growth increments, consisting of an inner light band and a narrower, sharply delineated, continuous outer dark band adjacent to it, were counted using a compound microscope with bright field illumination at 800 × or 1,250 × magnification. Faint bands inside the otolith nucleus in reared larvae and "subdaily" or weak rings between well-defined growth increments in some older (>30 d old) field-caught fish were not counted. Counts were made on only one sagitta of the pair and were repeated until a

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

final, "best" count was reached. Successive counts and verification counts which were made by the original reader at a later time usually did not vary by more than ±2. Age estimates could not be obtained for 10% of the field-caught larvae because increments were faint and indistinct or the otoliths were misshapen. Maximum otolith and nucleus diameters were measured to the nearest micron. Photomicrographs were taken at 500 × or 1,000 × magnification under a light microscope.

Shrinkage of larvae preserved in 80% ethanol was compared with shrinkage after preservation in 10% seawater-diluted Formalin, the fixative most commonly used to preserve plankton samples. Thirty 7-day-old reared larvae were measured alive and immediately preserved in either 80% ethanol (15) or 10% Formalin (15). The live, mean standard lengths of the two groups of larvae were 4.34 and 4.42 mm. After 4 mo in preservative the mean standard length of the ethanol-preserved group was 4.20 mm and of the Formalin-preserved group, 4.196 mm. Mean percent shrinkage or 100(original SL − preserved SL/original SL) was 3.2% in the ethanol-preserved group and 5.1% in the Formalin-preserved group. The difference in amount of shrinkage between the two groups was highly significant (ANOVA, $P<0.01$). Care must be taken, therefore, when comparing estimates of size at age based on measurements of larvae preserved in different fixatives. From this limited investigation it became apparent that Formalin-preserved *P. vetulus* larvae appear to be somewhat smaller at age than ethanol-preserved fish.

Statistical Procedures

Gompertz and von Bertalanffy growth models were fitted to larval *P. vetulus* data because the form of the length-age plot was nonlinear with a distinct upper asymptote. A detailed discussion of the Gompertz function, which is the primary model used in this paper, and methods for obtaining initial parameter estimates are presented by Zweifel and Lasker (1976). The generalized equation of this model is:

$$L_t = L_0 \exp\left[K\left(1 - e^{-\alpha t}\right)\right],$$

where L_t = length at age t; L_0 = length at $t = 0$ (i.e., where the curve intercepts the y-axis); and $K = \frac{A_0}{\alpha}$, or the specific growth rate at $t = 0$ divided by the rate of exponential decay. Untransformed data were used in this model because the standard deviation of larval lengths at age remained relatively constant and did not increase with age, indicating variance homogeneity within the data set. The Gallucci and Quinn (1979) version of the von Bertalanffy equation was employed, utilizing the new parameter, $w = kL_\infty$, where k is the growth constant, and L_∞, the asymptotic maximum size, which for *P. vetulus* larvae is the maximum size attained in the plankton prior to transformation into benthic juveniles. The general form of this equation is:

$$L_t = \frac{w}{k}\left\{1 - \exp\left[-k(t - t_0)\right]\right\},$$

where t_0 is the time when $L_0 = 0$ (i.e., where the curve intercepts the x-axis).

The SPSS NONLINEAR[4] program employing Marquardt's algorithm was used to fit both models. A measure of goodness of fit was provided by the residual sums of squares (RSS), the standard error of the regression (or standard deviation of the residuals), and approximate 95% confidence limits for each parameter assuming linearity. Linear confidence theory can be applied here because the assumption of linearity at the final (least squares) parameter values is a reasonable one (Conway et al. 1970; Kimura 1980). A comparison of the RSS at the final parameter values to the linear estimate RSS provides a measure of the linearity of the sum of squares (SS) function (SPSS NONLINEAR program).

Absolute growth rate or $\frac{L_2 - L_1}{t_2 - t_1}$ expressed in millimeters per day and specific growth rate or $\frac{\ln L_2 - \ln L_1}{t_2 - t_1} \times 100$ expressed as percent per day of length were calculated (Ricker 1979).

RESULTS

Increment Formation

Parophrys vetulus larvae survived and grew in the laboratory for over 35 d after hatching, with some individuals eventually transforming into juveniles. However, growth after yolk-sac absorption, between days 4 and 5, was retarded and

[4]SPSS NONLINEAR. Statistical Package for the Social Sciences, Vogelback Computing Center, Northwestern University, Evanston, IL 60201.

not comparable to growth in the field. Despite this, growth increments were visible on the otoliths of over 300 reared larvae. Increments, though extremely narrow and crowded, were even visible on the otoliths of larvae as old as 54 d.

In the laboratory, the highest incidence of larvae with one growth increment occurred on days 5 and 6 (Table 1; Fig. 1a, b). This coincided with the time that larvae first began to swim actively near the surface of rearing containers and search for food. By day 5 larvae had also acquired darkly pigmented, iridescent eyes and functional mouths, and had utilized all or almost all their yolk. Age at first increment formation in the field was ascertained by comparing mean otolith diameter (μm) of field-caught larvae with a single increment, to mean otolith diameter of laboratory-reared larvae of known age (Table 1). The otolith diameter, 23.8 μm, of field-caught larvae with only one growth increment ($\overline{SL}$ = 3.7 mm) fell between the mean values for laboratory-reared larvae at 5 d, 23.1 ($\overline{SL}$ = 4.2 mm), and at 6 d, 24.2 ($\overline{SL}$ = 3.9 mm). Age of all field-caught larvae with one otolith growth increment was, therefore, taken to be 6 d. Age at first increment formation varied among individuals in the laboratory and may, likewise, vary in the field; however, for the purpose of developing a generalized growth model, a single, best estimate of this event was made. The apparent smaller size of field-caught larvae with one increment most likely resulted from shrinkage during capture prior to preservation (Theilacker 1980). Larvae sampled in the laboratory were pipetted alive directly into preservative, thus reducing the amount of handling-induced shrinkage.

Although laboratory results were somewhat ambiguous, daily periodicity of otolith growth increment formation in *P. vetulus* was inferred from the following observations: 1) despite less than optimum rearing conditions some 14-, 17-, and 20-d-old larvae had added one increment each day since first formation on day 4 (Table 2); 2) no other periodical pattern in increment formation (i.e., other than daily) was observed among laboratory-reared larvae; 3) increment addition among larvae in the sea appeared to follow a stable and uniform pattern. The wide range in number of otolith increments among reared larvae of known age may have been caused by poor growing conditions which resulted in stunted body and otolith growth (Table 2). Reared larvae of northern anchovy also failed

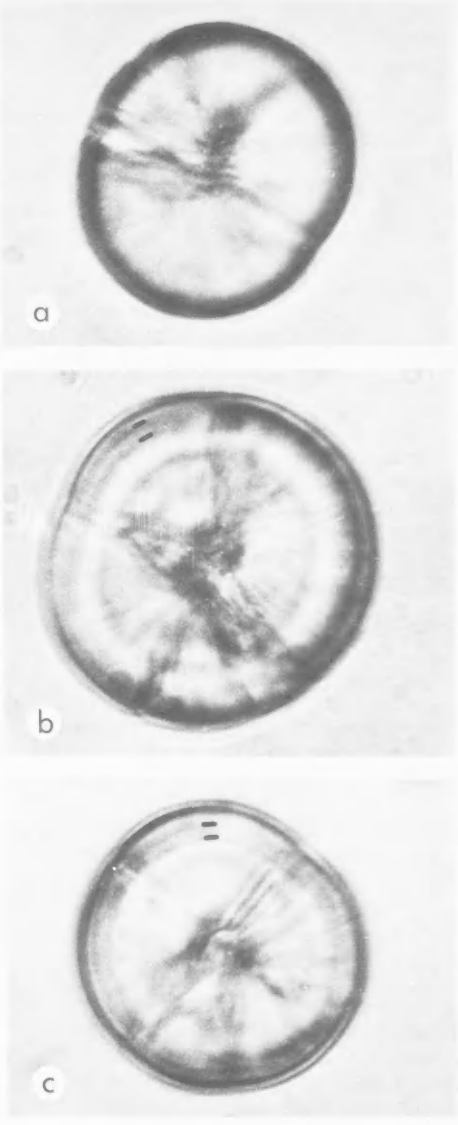

FIGURE 1.—Photomicrographs of *Parophrys vetulus* otoliths (× 1,000). a. Sagitta (22 μm in diameter) prior to first increment formation from a 4-d-old, laboratory-reared larva; b. Sagitta (24 μm in diameter) with two complete increments (highlighted with black lines) from a 6-d-old, laboratory-reared larva; c. Sagitta (22 μm in diameter) with two complete increments (highlighted with black lines) from a 7-d-old, field-caught larva.

TABLE 1.—Comparison of mean otolith diameters (OD) of laboratory-reared and field-collected *Parophrys vetulus* larvae. Age of reared larvae represents days from hatching.

Age (days)	Mean OD (μm)	No. larvae	No. growth increments 0	1	2	3	4	Mean OD (μm)	No. larvae	No. growth increments
0	14.6	10	10							
1	16.6	12	12							
2	18.8	10	9	1						
3	20.5	11	10		1					
4	21.6	14	13		1			21.3	7	0
5	23.1	24	10	10	4			23.8	4	1
6	24.2	19	4	4	8	2	1	24.6	10	2

to consistently form growth increments when maintained on low rations (Methot and Kramer 1979). In *P. vetulus*, delayed inception of increment formation, up to 8 d after hatching, may also have accounted for some of the apparent irregularity in increment formation in the laboratory (Table 2). Another factor contributing to ambiguity of laboratory results was the difficulty in counting otolith increments in older larvae. Increments in most laboratory-reared fish after 16-25 d were exceedingly faint and, in some fish, no increments could be discerned (Fig. 2a, b). Growth increments were, in general, clearer and more distinct on the otoliths of field-caught *P. vetulus* larvae than on otoliths of laboratory-reared fish (Figs. 1c, 2c). The steady increase in number of increments with increasing otolith diameter and length of pretransformation larvae in the field is evidence that the irregularity in increment formation observed in the laboratory did not occur under natural feeding conditions (Figs. 3, 4).

Age and Growth

Age of field-caught *P. vetulus* larvae in days from hatching was estimated by adding 5, the number of days prior to appearance of the first otolith growth increment, to the number of increments counted on sagittae. Counts of growth increments were obtained from 338 larval and transforming, pelagic specimens ranging from 2.4 to 20.0 mm SL (Fig. 4). But age could be estimated for only 331 larvae because increment formation had not yet begun in seven small specimens, 2.4-3.7 mm SL (Fig. 5). The oldest *P. vetulus* taken in plankton samples during 1977-78 was 74 d (2.4 mo) old and 17.8 mm SL. The next oldest larvae ranged from 65 to 70 d old and were 19-20 mm SL. The length of pelagic life of *P. vetulus* can be estimated directly from these data to be 2-2.5 mo. Few *P. vetulus* larvae >20 mm SL, the size at which larvae transform to benthic juveniles (Ahlstrom and Moser 1975; Rosenberg and Laroche footnote 3), were taken in extensive plankton collections off Oregon during the spring months in 1972-75 (Laroche and Richardson 1979). The largest larva taken in those collections was 22 mm SL.

Behavior of reared *P. vetulus* larvae further supports a pelagic phase of 2+ mo. At approximately 60 d of age, larval *P. vetulus* maintained in the laboratory first exhibited the tendency to rest on their sides on the bottom and to swim with their bodies at an angle to the vertical (J. L. Laroche unpubl. data).

TABLE 2.—Summary of growth in body length (SL) and otolith diameter (OD), and counts of growth increments on otoliths of laboratory-reared *Parophrys vetulus* larvae. *N* = number of larvae from which growth increment counts were taken; (*N*) = number of larvae used in mean otolith diameter calculation.

Age (days)	*N*	Mean SL (mm)	Range SL (mm)	Mean OD (μm)	Range OD (μm)	No. growth increments Mean	Range
4	14	4.1	3.7-4.4	21.6	20-25	0	0-2
5	24	4.2	3.8-4.5	23.1	20-25	1	0-2
6	19(17)	3.9	3.1-4.2	24.2	23-27	2	0-4
9	9	4.0	3.7-4.1	24.7	23-26	3	2-4
10	13	4.2	3.7-4.6	25.7	25-27	4	3-6
14	13	4.9	5.8-4.2	28.7	27-33	8	5-10
17	13	5.4	4.5-6.3	29.6	28-33	10	5-13
20	7(6)	5.7	5.1-6.4	31.8	30-36	10	5-16
21	6	5.9	5.4-6.6	31.2	30-34	13	10-16
26	18(17)	7.0	5.6-8.6	33.4	30-37	14	10-20

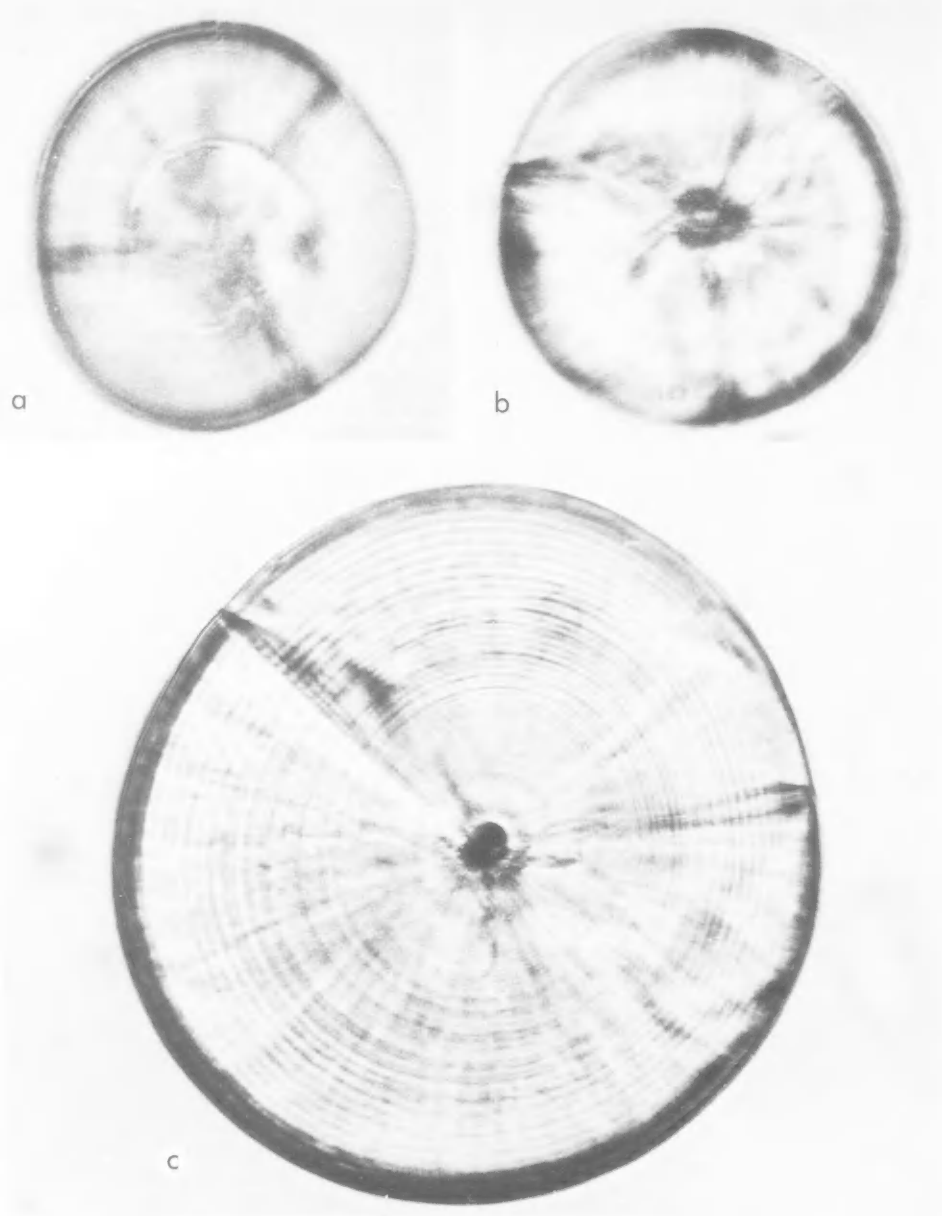

FIGURE 2.—Photomicrographs of *Parophrys vetulus* otoliths (×1,000). a. Sagitta (30 μm in diameter) with 16 complete increments from a 21-d-old, laboratory-reared larva; b. Sagitta (32 μm in diameter) with no discernible increments from a 22-d-old, laboratory-reared larva; c. Sagitta (102 μm in diameter) with 42 complete increments from a 47-d-old, field-caught larva.

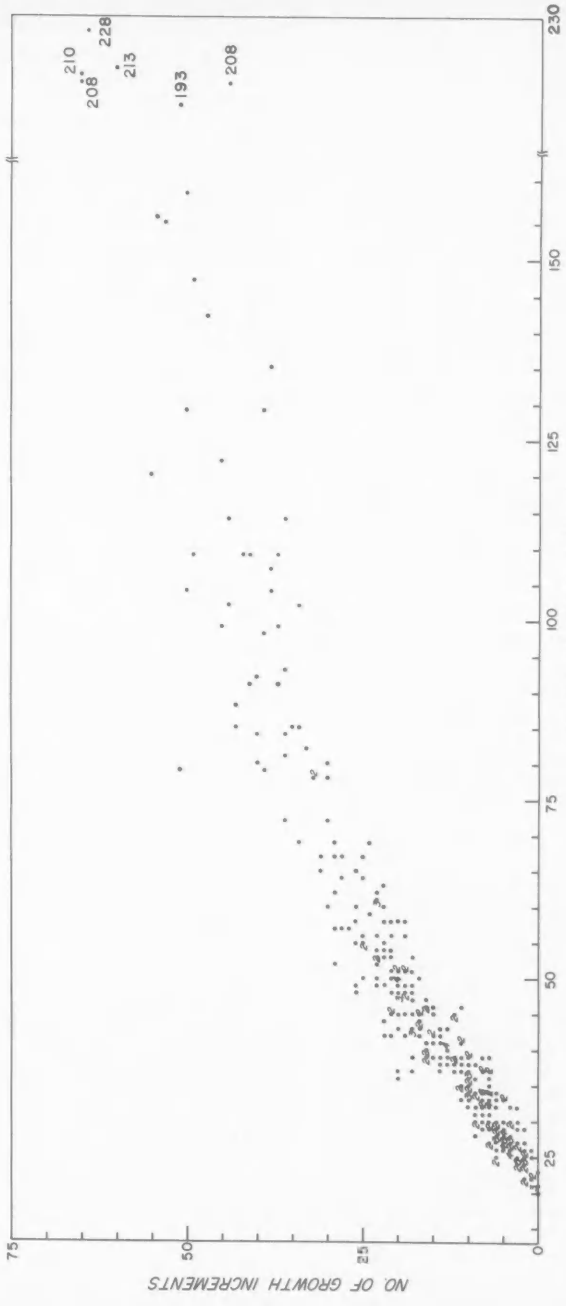

FIGURE 3.—Number of otolith growth increments related to otolith diameter of 338 larval and transforming, field-caught *Parophrys vetulus*.

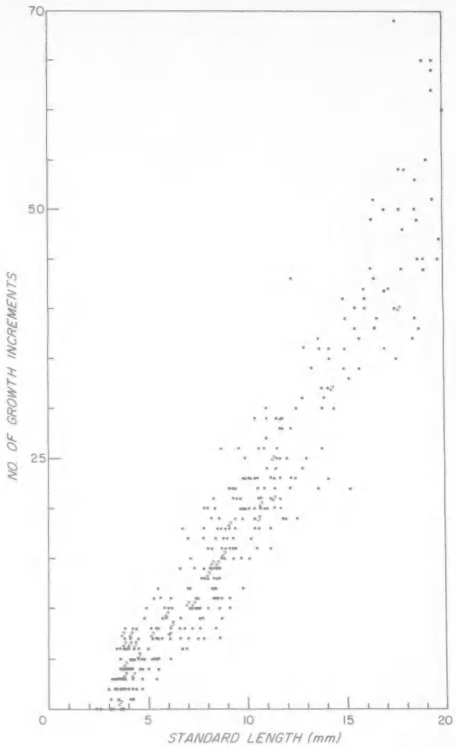

FIGURE 4.—Number of otolith growth increments related to standard length of 338 larval and transforming, field-caught *Parophrys vetulus*.

Our description of early growth of *P. vetulus* in Oregon coastal waters at temperatures ranging from 9° to 11°C is based on the ages and lengths of 331 specimens, 3.1-20.0 mm SL, with otolith growth increments. Gompertz and von Bertalanffy models yielded good and nearly identical fits to the data and similar estimates of growth rate; therefore, the results of only one model (Gompertz) are presented (Table 3; Fig. 5). RSS and linear estimate RSS of the Gompertz growth parameters were very similar; thus, the assumption of linearity in computing 95% confidence limits is reasonable, and the computed limits indicate relatively narrow confidence regions around the parameters (Table 3).

Previous estimates of age at length of larval *P. vetulus* were derived from the progression of modes in length-frequency distributions of larvae from a time series of (10% Formalin preserved) plankton samples (Laroche and Richardson 1979). A comparison of those results with age at length estimated by the Gompertz equation (Zwiefel and Lasker 1976) indicates that the length-frequency method overestimated the age of larvae >5.5 mm SL by 2-3 times (Table 4).

Estimates of specific and absolute rates of growth were calculated from length at age for various ages as predicted by the Gompertz model (Table 5). Specific growth rate steadily decreased between 8 and 74 d. Absolute growth rate was fairly uniform between 8 and 31 d, slowed somewhat between 31 and 41 d, but was more drastically reduced between 73 and 74 d, at which time larvae undergo transformation, a

TABLE 3.—Gompertz equation and estimated parameters describing the growth of 331 *Parophrys vetulus* larvae in Oregon waters during the 1977-78 spawning season. RSS = residual sum of squares; SE = standard error of the regression; S^2 = variance; CL = confidence limits.

Equation $L_t = 2.073 \exp\left[2.354\,(1-e^{-0.045t})\right]$

Parameters	S^2	RSS	Linear est. RSS	RSS 520.83 / SE 1.256 Approximate 95% CL
$L_0 = 2.073$	0.023	564.892	564.892	$L_1 = 1.779$, $L_2 = 2.367$
$K = 2.354$	0.003	535.762	536.093	$L_1 = 2.245$, $L_2 = 2.462$
$\alpha = 0.045$	0.00001	533.854	533.635	$L_1 = 0.040$, $L_2 = 0.050$

TABLE 4.—Age of *Parophrys vetulus* larvae; (*A*) estimated from modal progression in length-frequency distributions of larvae caught during 1971 in biweekly and weekly Formalin-preserved plankton samples (Laroche and Richardson 1979), (*B*) estimated by the Gompertz equation based on otolith increment counts from ethanol-preserved larvae caught in 1977-78.

	Estimated age (weeks)	
SL (mm)	(*A*)	(*B*)
5.5	2.3	1.7
7.5	4.1	2.5
9.5	5.9	3.3
11.5	8.7	4.1
13.5	13.4	5.0
15.5	17.6	6.1
17.5	21.9	7.5

TABLE 5.—Growth rates of *Parophrys vetulus* larvae predicted from the Gompertz equation at various times from hatching.

Age (days)	Specific growth rate (% per day SL)	Absolute growth rate (mm per day)
8-9	7.3	0.32
15-16	5.3	0.36
19-20	4.4	0.36
24-25	3.5	0.35
30-31	2.7	0.33
40-41	1.7	0.25
73-74	0.4	0.08

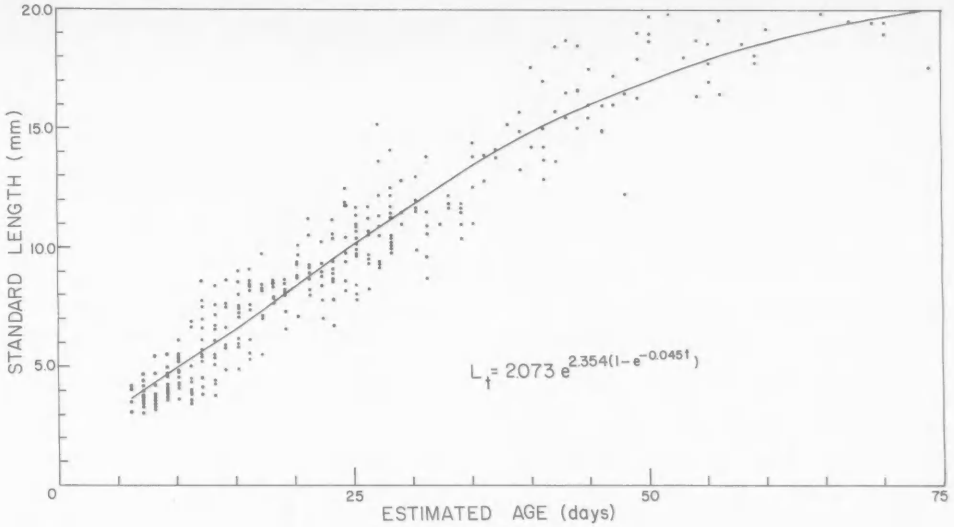

FIGURE 5.— Gompertz curve and equation fitted to length at age of 331 larval and transforming, field-caught *Parophrys vetulus* with at least one otolith growth increment.

period characterized by reduced growth in length (Rosenberg and Laroche 1982).

The plot of otolith diameter on standard length of pelagic larval and transforming *P. vetulus* revealed an allometric relationship (Fig. 6). A distinctive feature of this plot was the apparent continued, even accelerated growth of sagittae as *P. vetulus* larvae reached the size of transformation, 18-20 mm SL, when rate of growth in body length slows down. Physical evidence of accelerated growth in otolith diameter relative to body length can be seen by the increased width of the outermost increments on otoliths of larvae older than 30 d (e.g., outer 9-10 increments on sagitta in Fig. 2c). The otolith diameter to standard length relationship, once a mathematical formulation has been computed, can be used to back-calculate individual growth histories of larvae and juveniles (Rosenberg 1980; Methot in press), as has been done for adult fishes (Tesch 1968; Ricker 1969).

DISCUSSION

As in numerous other temperate and some tropical species of fishes, growth increments on the otoliths of *P. vetulus* larvae appear to be formed daily after yolk-sac absorption when larvae become capable of exogenous feeding. Counts of these increments provide more precise and accurate estimates of larval age and growth rates throughout the larval period than have previously been available. This information, when combined with abundance data, allows computation of age-dependent mortality rates resulting in more accurate estimates of larval mortality in the sea.

Empirically, both the Gompertz and von Bertalanffy growth models fit the larval *P. vetulus* data well. Both yielded similar values for length at age and growth rates from which age-dependent mortality estimates can be made. There has been much disagreement, on theoretical grounds, as to the appropriateness of either model for describing growth in fishes, although they are mathematically quite similar (e.g., Zweifel and Lasker 1976; Ricker 1979). Despite numerous attempts to attribute biological significance to mathematical models of growth, the best criterion available for choosing a particular model is still goodness of fit to the data (Ricker 1979). In that respect, both models were appropriate to this data set.

A practical measure of the appropriateness of mathematical models is the relative accuracy and stability of pertinent parameter estimates (Gallucci and Quinn 1979). In the Gompertz

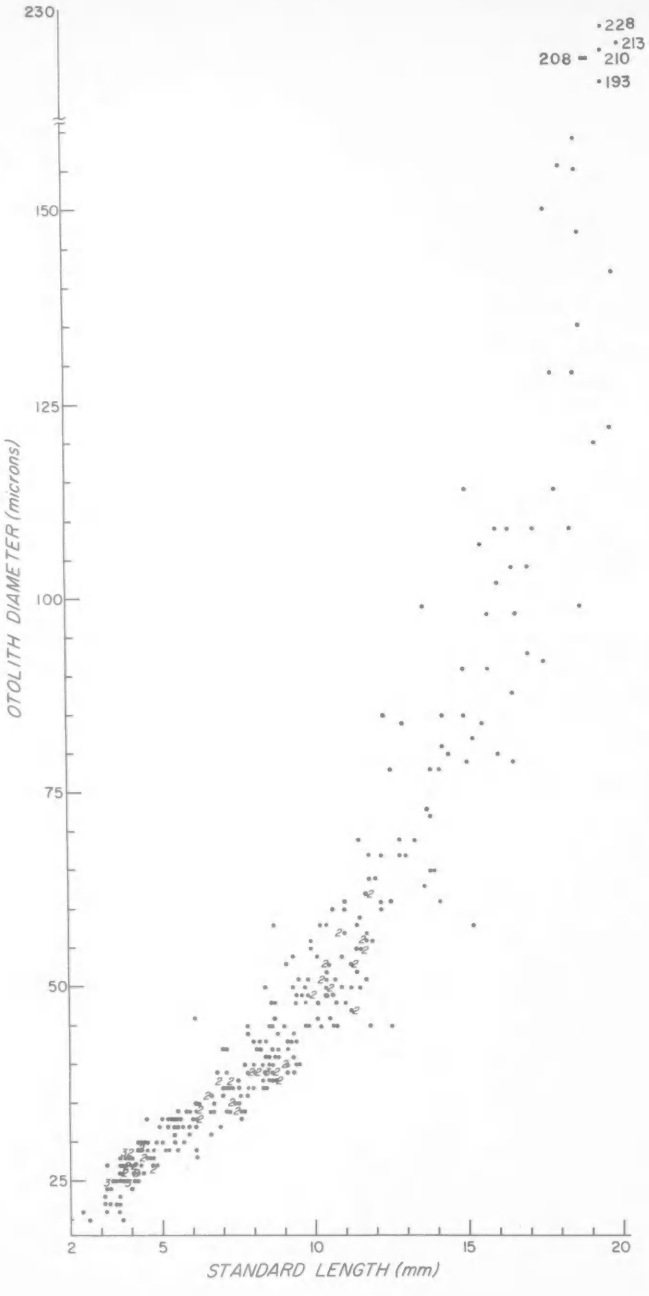

FIGURE 6.—Otolith diameter related to standard length of 338 larval and transforming, field-caught *Parophrys vetulus*.

model, the parameter L_0 or the y-intercept has been used as an estimator of length at hatching (Zweifel and Lasker 1976). However, the value of this parameter, 2.07 mm SL, for the *P. vetulus* data set was low compared to mean hatching lengths of reared larvae: 2.60 ($N = 11$) and 2.91 ($N = 10$) mm SL at 12°-13°C (Laroche unpubl. data); and 2.85 ($N = 25$) mm TL at 10°-11°C (Orsi 1968). Net-caught larvae on which the growth model is based would appear smaller at age because of increased shrinkage during capture (Theilacker 1980). This may account for some of the difference in predicted and observed hatching lengths. Another probable cause of this discrepancy is the lack of data points in the <6 d of age region of the plot, i.e., before growth increment formation begins. The value of L_0 is based on extrapolation beyond the actual data and may be, therefore, of questionable use as a measure of the appropriateness of this model.

Comparison with larval growth in the field at similar temperatures of another pleuronectid, *Pseudopleuronectes americanus*, provided evidence that growth rates predicted by the Gompertz model for *Parophrys vetulus* are realistic. Larval *Pseudopleuronectes americanus* between the ages of 28 and 42 d, growing in large enclosures in Narragansett Bay at 10°-15°C, had a specific growth rate of 1.9% per day of standard length (Laurence et al. 1979). The predicted specific growth rate of *Parophrys vetulus* of the same age, growing at 9°-11°C, was 2.2%. Larval *Pseudopleuronectes americanus* between 28 and 42 d of age grew from 6.6 to 8.6 mm SL, while *Parophrys vetulus* larvae grew from 11.2 to 15.3 mm SL. Although these two species differ in size at age, both transform at approximately the same age, 8-10 wk, and appear to grow at similar rates between 4 and 6 wk of age. Since length at hatching, ~2-3 mm SL, is similar for both species, higher rates of growth prior to and after 4-6 wk probably accounts for the greater size at age of *P. vetulus* and greater size at transformation, >18 mm SL in *P. vetulus* versus <10 mm for *Pseudopleuronectes americanus*.

A comparison of otolith-estimated and length-frequency derived age-at-length data indicated that the latter method overestimated age of *Parophrys vetulus* larvae >5.5 mm SL by 2-3 times. This resulted in a gross overestimate of duration of the pelagic life of this species, 18-22 wk (Laroche and Richardson 1979) compared to 8-10 wk based on the age data presented here. It is unlikely that these large differences are solely the result of different preservatives. Such a large discrepancy between the two methods demonstrates the serious inaccuracies that could result from attempts to estimate age and growth rates from length-frequency data. Such data predictably yield low estimates of growth, especially for species with protracted spawning, because of continual recruitment of small larvae to the population. Problems of net avoidance by larger specimens further bias length-frequency distributions.

The otolith aging method developed in this study could be used further to investigate growth and survival among different cohorts of *P. vetulus* larvae. Spawning in this species is highly variable in both frequency and timing (Laroche and Richardson 1979). Peak spawning can be bimodal in some years with a 2-4 mo separation between peaks (Kruse and Tyler[5]). Larvae produced in those two peaks could develop and grow under very different temperature regimes and feeding conditions, which could result in two distinct groups of larvae differing in rates of growth, mortality, and relative contribution to that year class.

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[5]Kruse, G. H., and A. V. Tyler. 1980. Influence of physical facotrs on the English sole (*Parophrys vetulus*) spawning season. Unpubl. manuscr., 25 p. Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331.

and their microscope for otolith observations. Otolith photomicrographs were taken with the help and guidance of Michael D. Richardson, Naval Ocean Research and Development Activities, Bay St. Louis, Miss.

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LITERATURE CITED

AHLSTROM, E. H., AND H. G. MOSER.
1975. Distributional atlas of fish larvae in the California Current region: flatfishes, 1955 through 1960. Calif. Coop. Oceanic Fish. Invest. Atlas 23, 207 p.

BAGENAL, T. B., AND E. BRAUM.
1971. Eggs and early life history. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, 2d ed., p. 166-198. IBP (Int. Biol. Programme) Handb. 3.

BROTHERS, E. B., AND W. N. MCFARLAND.
In press. Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts [*Haemulon flavolineatum* (Desmarest), Haemulidae]. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 178.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

CONWAY, G. R., N. R. GLASS, AND J. C. WILCOX.
1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51:503-507.

DEGENS, E. T., W. G. DEUSER, AND R. L. HAEDRICH.
1969. Molecular structure and composition of fish otoliths. Mar. Biol. (Berl.) 2:105-113.

GALLUCCI, V. F., AND T. J. QUINN, II.
1979. Reparameterizing, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108:14-25.

KIMURA, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull., U.S. 77:765-776.

LAROCHE, J. L., AND S. L. RICHARDSON.
1979. Winter-spring abundance of larval English sole, *Parophrys vetulus*, between the Columbia River and Cape Blanco, Oregon during 1972-1975, with notes on occurrences of three other pleuronectids. Estuarine Coastal Mar. Sci. 8:455-476.

LAURENCE, G. C., T. A. HALAVIK, B. R. BURNS, AND A. S. SMIGIELSKI.
1979. An environmental chamber for monitoring "in situ" growth and survival of larval fishes. Trans. Am. Fish. Soc. 108:197-203.

METHOT, R. D., JR.
In press. Spatial covariation of daily growth rates of larval nothern anchovy, *Engraulis mordax*, and northern lanternfish, *Stenobrachius leucopsarus*. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178.

METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.

ORSI, J. J.
1968. The embryology of the English sole, *Parophrys vetulus*. Calif. Fish Game 54:133-155.

PANNELLA, G.
1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.
1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. *In* T. B. Bagenal (editor), The proceedings of an international symposium on the ageing of fish, p. 28-39. Unwin Brothers, Surrey, Engl.

RICKER, W. E.
1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Board Can. 26:479-541.
1979. Growth rates and models. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, Vol. VIII, p. 677-742. Acad. Press, N.Y.

ROSENBERG, A. A.
1980. Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery grounds. M.S. Thesis, Oregon State Univ., Corvallis, 51 p.

ROSENBERG, A. A., AND J. L. LAROCHE.
1982. Growth during metamorphosis of English sole, *Parophrys vetulus*. Fish. Bull., U.S. 80(1):150-153.

STRUHSAKER, P., AND J. H. UCHIYAMA.
1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

TAUBERT, B. D., AND D. W. COBLE.
1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica*. J. Fish. Res. Board Can. 34: 332-340.

TESCH, F. W.
1968. Age and growth. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, 2d ed., p. 93-123. IBP (Int. Biol. Programme) Handb. 3.

THEILACKER, G. H.
1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull., U.S. 78:685-692.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

PHENOTYPIC DIFFERENCES AMONG STOCKS OF HATCHERY AND WILD COHO SALMON, *ONCORHYNCHUS KISUTCH*, IN OREGON, WASHINGTON, AND CALIFORNIA[1]

R. C. HJORT AND C. B. SCHRECK[2]

ABSTRACT

Similarities in phenotypic characters (isozyme gene frequencies, life history, and morphology) among 35 stocks of coho salmon, *Oncorhynchus kisutch*, from Oregon, Washington, and California were compared by using agglomerative and divisive cluster analyses. Coho salmon stocks from similar environments were phenotypically similar. Five groups of stocks were identified by the agglomerative cluster analysis: 1) wild stocks from the northern Oregon coast, 2) wild stocks from the southern Oregon coast, 3) stocks from hatcheries that used wild coho salmon for an egg and sperm source, 4) stocks from large stream systems, and 5) hatchery stocks from the northern Oregon coast. Three trends were indicated by the clustering patterns: 1) stocks that were geographically close tended to be phenotypically similar, 2) stocks from large stream systems were more similar to each other than to stocks from smaller stream systems, independent of geographic proximity, and 3) hatchery stocks were more similar to each other than to wild stocks, and wild stocks were more similar to each other than to hatchery stocks. These trends may be useful to fishery managers for selecting donor stocks from hatcheries for transplanting to stream systems or transferring to other hatcheries. Individual phenotypic characters were correlated with characters of the stream systems. Results of two agglomerative cluster analyses, one of certain characters of the stocks and one of certain characters of the stream systems, demonstrated a lack of correspondence between stream types and stock phenotypes.

Genetic diversity among stocks of anadromous salmonids (Simon and Larkin 1970) is a biological characteristic that is more frequently discussed than used in fishery management. The tendency to return to native streams reduces gene flow among salmon populations and enables the individual stocks to adapt to the native stream systems. The mixing of stocks highly adapted to their native stream systems with other stocks, or transplanting them to other stream systems, may reduce the rate of return or survival rate of the donor stock (Ritter 1975[3]; Bams 1976). If the survival rate of a salmon stock is related to its degree of adaptation to its stream system, fishery managers may be able to increase survival of hatchery fish by planting them in recipient streams having native stocks genetically similar to the planted fish. Higher survival should be especially important during the first several generations, while the transplanted stock is adapting to the recipient environment. An additional advantage of using genetically similar stocks might be a reduction in the introgression of divergent hatchery genotypes into wild stocks (Reisenbichler and McIntyre 1977).

Genetic descriptions of salmon stocks could benefit salmon management by assisting fishery managers in selecting hatchery stocks and in protecting wild stocks. Obviously, determination of genetic similarity among stocks is not now possible for the entire genome; however, similarity can be estimated by comparing genetically related characters. Two biochemical characters that vary among stocks of coho salmon, *Oncorhynchus kisutch*, are transferrin (Utter et al. 1970) and phosphoglucose isomerase (PGI) (May 1975), the electrophoretic expressions both of which were established by breeding studies to be genetically determined. Life history and morphological characters also vary among salmonid stocks. Time of spawning (Roley 1973) and frequency of occurrence of jacks in the population (Feldmann 1974) both have a genetic basis in

[1]Oregon State University Agricultural Experiment Station Technical Paper Number 5477.

[2]Oregon Cooperative Fishery Research Unit, Oregon State University, Corvallis, OR 97331. Cooperators are Oregon State University, Oregon Department of Fish and Wildlife, and U.S. Fish and Wildlife Service.

[3]Ritter, J. A. 1975. Lower ocean survival ratio for hatchery reared Atlantic salmon (*Salmo salar*) stocks released in rivers other than their native streams. Int. Counc. Explor. Sea, Anadromous and Catadromous Fish Comm., C. M. 1975/M 26, 10 p.

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FISHERY BULLETIN: VOL. 80, NO. 1, 1982.

coho salmon but probably have an environmental component as well. A genetic basis, as shown in rainbow trout, *Salmo gairdneri*, has also been established for numbers of vertebrae (Winter et al. 1980a), scales in the lateral series (Winter et al. 1980a), scale rows (Neave 1944), gill rakers (Smith 1969), branchiostegals (MacGregor and MacCrimmon 1977), and anal fin rays (MacGregor and MacCrimmon 1977). Ricker (1970) hypothesized that the meristic characters of salmonids probably have both genetic and environmental components. The difficulty of determining the importance of these phenotypic characters to the fitness of the stock does not preclude the possibility that they could, through selection or pleiotrophic effects, have a bearing on fitness as suggested by Barlow (1961).

The objective of this study was to characterize stocks of coho salmon by using enzyme gene frequencies, life history characters, and morphological characters. Secondarily, we hoped this information would help provide a basis for selecting donor stocks in Oregon hatchery programs. The stocks were selected so that comparisons could be made among geographical areas and stream types and between hatchery and wild stocks. We calculated a measure of a phenotypic similarity and used cluster analysis to display the relationships among stocks. Because cluster analyses are arbitrary (Blackith and Reyment 1971), we used two clustering strategies. Factors affecting genetic similarity were hypothesized by determining environmental characteristics common to the similar stocks.

Although our analysis is primarily systematic, we correlated the phenotypic characters with variables characteristic of the stream systems. Although correlations do not prove a functional significance, they are included here because inferences and hypotheses can be developed from the correlations for future studies.

METHODS

Sampling

We evaluated 10 characters for 15 hatchery stocks (based on samples of 75-100 juvenile coho salmon of the 1976 brood from 14 hatcheries in Washington, Oregon, and California and 9 hatcheries from Oregon for the 1977 brood year) and 12 wild stocks (based on samples of 30-100 juvenile coho salmon of the 1976 and 1977 broods, collected by electrofishing from 12 Oregon stream systems). (See Figure 1 for locations of hatcheries and stream systems.) Because some of the hatcheries have used nonnative egg sources, and stream systems have been stocked with juvenile and adult coho salmon, few pure native stocks remain. We did not use hatchery stocks or

FIGURE 1.—Map indicating sample site locations of wild and hatchery coho salmon stocks. Location codes are as follows with the hatcheries in parentheses: ALSE, Alsea River (Fall Creek Hatchery); BEAV, Beaver Creek; BIGC, Big Creek (Big Creek Hatchery); COLM, Columbia River (Cascade Hatchery in 1976 and Bonneville Hatchery in 1977); COQL, Coquille River; COWL, Cowlitz River (hatchery stock reared at Cascade Hatchery in 1976 and Big Creek Hatchery in 1977); KLAM, Klamath River (Irongate Hatchery); MADR, Mad River (Mad River Hatchery); NEHA, Nehalem River; NEST, Nestucca River; NONE, North Nehalem River (North Nehalem River Hatchery); QUIL, Quilcene River (Quilcene River Hatchery); QUIN, Quinault River Hatchery); ROGU, Rogue River (Cole Rivers Hatchery); SALM, Salmon River Hatchery); SAND, Sandy River (Sandy River Hatchery); SILZ, Siletz River; TENM, Tenmile Lakes; TRAS, Trask River (Trask River Hatchery); TRIN, Trinity River (Trinity River Hatchery); UMPQ, Umpqua River (hatchery stock collected from Smith River and reared at Cole Rivers Hatchery).

fish from tributaries of streams that had received a large supplement of a nonnative hatchery stock in the previous 6 yr. This was to ensure that characterization of the genotype would reflect environmental considerations rather than introgression of foreign stocks.

Morphological Characters

For each sample, 15 carcasses were frozen for later counts. Scales in the lateral series were counted in the second row above the lateral line, starting with the anteriormost scale and terminating at the hypural plate. Scales above the lateral line were counted from the anterior insertion of the dorsal fin to the lateral line. Anal ray counts did not include the short rudimentary anterior rays, and branched rays were counted as one. The total number of gill rakers on the first gill arch was recorded. Alizarin red was used to highlight rudimentary gill rakers. The total number of branchiostegal rays from both sides was counted. Vertebral counts, made on X-ray plates, included the last three upturned centra. Accuracy of morphological counts was checked by recounting two fish from each sample. If errors were found, additional fish from that sample were recounted to correct for any error.

Electrophoresis

Blood and white muscle samples were collected from the fish that were not used for morphological counts. The caudal peduncle was severed and the blood collected in heparinized microhematocrit tubes that were then centrifuged and stored at −10°C. White muscle samples (1 cm^3) were removed from the anterior dorsal portion of the frozen carcasses, homogenized with 2 or 3 drops of water, and then centrifuged to clear the supernatant. Only the blood serum and supernatant were used for electrophoresis.

The methodology for electrophoresis of transferrin and phosphoglucose isomerase followed the basic principles of May (1975) with some modifications by Solazzi.[4] The gel and elctrode buffers were described by Ridgway et al. (1970). Four genotypes of transferrin (AA, AC, CC, and BC) in the serum samples were interpreted according to Utter et al. (1970). Transferrin was recorded as the frequency of the "A" allele, since the "B" allele was relatively rare. The variant allele for the second locus of phosphoglucose isomerase, first observed in white muscle tissue by May (1975), was recorded as the frequency of this variant allele.

Life History

The life history characters we used were time of peak spawning and proportion of females in the adult population. We estimated the peak spawning times on the basis of interviews with district fishery biologists and hatchery managers. Whenever possible, we verified the estimates with spawning ground survey records and hatchery records. We stratified the peak spawning times into five segments of 2 wk each.

The proportions of adult females (3 yr olds) were estimated from hatchery records and spawning ground surveys. This character is an indirect measure of the proportion of jacks (males that mature at 2 yr of age) in the population. Populations with high proportions of jacks in a given year should have relatively higher proportions of females returning the next year. A direct measure of the proportion of jacks cannot be used because body size differences between jacks and 3-yr-old adults affect the catch in gill net fisheries, retention in hatchery holding ponds, recovery of carcasses on spawning ground surveys, and catch rate in sport fisheries.

Environmental Data

Stream characteristics include distance upstream to spawning grounds, basin area, area and length of the estuary on the stream system, latitude, gradient, spring runoff, the presence or absence of the myxosporidan parasite, *Ceratamyxa shasta*, and the presence or absence of the following nine species of fish: carp, *Cyprinus carpio*; Oregon chub, *Hybopsis crameri*; northern squawfish, *Ptycholcheilus oregonensis*; speckled dace, *Rhinichthys osculus*; redside shiner, *Richardsonius balteatus*; largescale sucker, *Catostomus macrocheilus*; brown bullhead, *Ictalurus nebulosus*; largemouth bass, *Micropterus salmoides*; and striped bass, *Morone saxatilis*. To separate the populations that have short and potentially long swimming distances to the spawning grounds, we measured spawning distances from the mouth of the stream sys-

[4]Solazzi, M. F. 1977. Methods manual for the electrophoretic analysis of steelhead trout (*Salmo gairdneri*). Oreg. Dep. Fish Wildl., Res. Sect., Inf. Rep. Ser. Fish. 77-7, 35 p.

tem to the upper limit of coho salmon spawning, as estimated from Anadromous Fish Distribution Maps[5] and interviews with district fishery biologists. Inasmuch as, intuitively, latitude should be correlated with the temperature and flow regimes of the stream systems, we determined the latitude at the mouth of each stream system. Gradients were calculated from tidewater to the upper limit of coho spawning as a basis for estimating the difficulty of the spawning migration. Because estuary size and length is an estimate of exposure to vibriosis (Harrel et al. 1976) and potential richness of feeding grounds (Myers 1979), we measured the estuary lengths, stream elevations, and distances on United States Geographical Survey Quadrangle Maps. Inasmuch as high flows could have an effect on both the early life history and the smolting processes of juvenile coho salmon, we determined the presence of a spring runoff from snowmelt by interviewing district biologists. We obtained information on the distributions of other fish species in Oregon stream systems from C. E. Bond,[6] and on the distribution of *Ceratamyxa shasta* from J. E. Sanders.[7]

We obtained temperature data from hatchery records to help interpret the morphological data for the hatchery stocks. The average temperature for the first month of incubation was used, because previous studies have indicated that this time is a period during ontogeny when morphological features may be most sensitive to the effects of temperature (Tåning 1952).

Statistics

We calculated averages for the morphological characters, enzyme gene frequencies, and the proportion of females for each stock, and used multivariate analysis of variance and Rao's (1970) test for additional information to determine whether morphological characters differed significantly among stocks. In Rao's test, the statistical significance of each morphological character is determined, given that the other morphological characters are already in the model. Because environmental data on spawning distance, estuary length, estuary size, basin area, and gradient were skewed, we transformed them to natural logarithms to stabilize the variance and improve normality. We standardized the stock characters ($\bar{z} = 0$, $S^2 = 1$) for the cluster analyses, using the standard normal standardization. This standardization expresses the stock character as standard deviations from the character means, thus giving equal weight to each character.

We calculated correlation coeffients (Snedecor and Cochran 1967) between the stock characters and the environmental data for all stocks, and between the morphological characters and temperature data for hatchery stocks only. The levels of significance for the correlation coefficients were also calculated as described by Snedecor and Cochran (1967).

We used two cluster analysis programs to display similarities among stocks. One, a nonhierarchical divisive cluster analysis, minimized the total sum of squares between observations and the cluster means (McIntire 1973). In the other, a hierarchical agglomerative cluster analysis, Euclidean distance was used as the dissimilarity measure, and the clustering strategy was group average (see Sneath and Sokal [1973] or Clifford and Stephenson [1975] for terminology). Standardized data were used in both programs.

We used canonical variate analysis to investigate the relation among the clusters from the agglomerative cluster analysis (Clifford and Stephenson 1975). Canonical variate analysis produces canonical variables that project groups of multivariate data onto axes separating the groups as much as possible. We plotted the canonical variables against each other in two-dimensional space to determine the relationships among clusters and the discreteness of the clusters.

RESULTS AND DISCUSSION

Morphological Characters

Significant differences ($\alpha = 0.01$) for each morphological character (Tables 1-3) as indicated by multivariate analysis of variance and Rao's test of additional information existed among the 35 samples which consisted of wild and hatchery stocks from two brood years. When morphological characters for each stock between brood years were compared for each of the hatcheries that were sampled in both years of the study

[5]Anadromous Fish Distribution Maps. Oregon State Water Resources Board, Salem, Oreg.

[6]Carl E. Bond, Professor of Fisheries, Oregon State University, Corvallis, OR 97331, pers. commun. April 1979.

[7]James E. Sanders, Assistant Fish Pathologist, Oregon Dep. Fish Wildl., Corvallis, OR 97331, pers. commun. February 1979.

TABLE 1.—Means, standard errors (in parentheses), and ranges for the morphological characters of the 1976 brood year hatchery samples of juvenile coho salmon and the hatchery water incubation temperatures for the first month of incubation. Sample sizes were 15. The data are listed in north to south order of the sampling locations.

Stock and (in parentheses) incubation water temperatures (°C)	Scales in lateral series	Scales above lateral line	Anal rays	Gill rakers	Branchiostegals	Vertebrae
Washington:						
Quilcene River Hatchery (7.3)	126.93 (.97) 116-132	28.13 (.38) 25-30	14.07 (.15) 13-15	22.33 (.19) 21-23	27.87 (.26) 26-30	64.40 (.13) 64-65
Quinault River Hatchery (7.3)	132.67 (.48) 130-136	29.93 (.33) 28-32	13.53 (.16) 13-15	22.53 (.24) 21-24	26.67 (.21) 25-28	65.50 (.13) 65-66
Oregon:						
Cascade Hatchery (6.9) (Columbia River)	133.07 (.56) 128-135	28.20 (.40) 26-32	14.00 (.20) 12-15	22.20 (.35) 20-25	27.27 (.37) 25-29	66.80 (.22) 66-68
Big Creek Hatchery (6.4) (Columbia River)	132.67 (.57) 128-136	28.80 (.28) 28-31	14.31 (.13) 13-15	22.87 (.17) 22-24	26.07 (.30) 24-28	65.80 (.15) 65-67
Cowlitz Hatchery stock, Cascade Hatchery (6.9)	133.60 (.63) 131-137	27.87 (.24) 26-29	13.80 (.14) 13-15	22.20 (.26) 21-24	28.13 (.24) 27-30	64.47 (.22) 65-68
Sandy River Hatchery (7.0) (Columbia River)	133.13 (.72) 128-137	28.27 (.42) 24-30	14.33 (.13) 14-15	22.07 (.34) 20-25	28.20 (.26) 26-30	66.07 (.21) 65-67
North Nehalem River Hatchery (7.8)	131.93 (.64) 128-138	28.33 (.30) 26-36	14.00 (.14) 13-15	22.67 (.27) 21-24	26.73 (.32) 24-28	65.80 (.17) 65-67
Trask River Hatchery (9.8)	132.13 (.48) 128-135	28.80 (.47) 26-32	13.93 (.12) 13-15	22.13 (.31) 20-24	26.40 (.32) 24-29	66.07 (.18) 65-67
Salmon River Hatchery (6.2)	129.40 (.54) 125-132	27.00 (.59) 23-33	13.60 (.19) 13-15	22.13 (.24) 21-24	25.40 (.24) 24-27	64.93 (.30) 62-66
Fall Creek Hatchery (5.7) (Alsea River)	132.00 (.50) 129-135	28.67 (.29) 27-31	14.00 (.17) 13-15	23.20 (.20) 22-25	27.13 (.34) 25-29	65.80 (.17) 65-67
Umpqua Hatchery stock (Smith River), Cole Rivers Hatchery (3.5)	131.20 (.51) 127-134	26.00 (.34) 24-28	13.47 (.19) 13-15	22.13 (.22) 21-23	25.13 (.24) 24-26	65.33 (.23) 64-67
California:						
Irongate Hatchery (5.3) (Klamath River)	132.73 (.78) 129-138	29.07 (.18) 28-30	13.80 (.14) 13-15	22.33 (.25) 21-24	27.00 (.28) 25-28	66.07 (.30) 64-68
Trinity River Hatchery (7.3) (Klamath River)	130.87 (.75) 126-137	28.27 (.64) 24-33	13.60 (.13) 13-14	22.00 (.31) 19-23	26.00 (.59) 20-28	66.00 (.14) 65-67
Mad River Hatchery (8.5)	129.20 (.88) 121-134	25.27 (.37) 22-27	13.40 (.19) 12-15	20.93 (.33) 19-23	23.47 (.51) 20-27	65.60 (.31) 63-68

(Table 4), the agreement between brood years was not particularly high, especially for scale rows and branchiostegal ray counts.

Although meristic counts and water temperatures during the incubation period of the eggs are usually correlated (Barlow 1961), we found that lateral series scale counts provided the only meristic character significantly ($\alpha = 0.05$) correlated with the temperature of the hatchery water during incubation. Under the extant environmental conditions, incubation temperatures may have little effect in determining the morphological characters of our stocks.

Among all possible statistically significant correlations between morphological characters and the stream characteristics in Table 5, only vertebral number and estuary length, and vertebral number and spawning distance, had correlation coefficients $>r = 0.50$ (Table 6). All other correlations each accounted for <25% of the variation observed. Possibly we overlooked some important environmental gradients, or possibly the selective forces occur during periodic environmental extremes or pulses that were not accounted for in our environmental data. Each of the counts significantly correlated with at least two of the characters of the stream systems, suggesting that, if these characters are the

TABLE 2.—Means, standard errors (in parentheses), and ranges for morphological characters of the 1977 brood year hatchery samples of juvenile coho salmon and the hatchery water incubation temperatures for the first month of incubation. Sample sizes were 15. The data are listed in north to south order of the sampling location.

Stock and (in parentheses) incubation water temperatures (°C)	Scales in lateral series	Scales above lateral line	Anal rays	Gill rakers	Branchiostegals	Vertebrae
Bonneville Hatchery (5.4)	133.33	26.73	13.93	22.53	27.00	65.80
(Columbia River)	(.61)	(.27)	(.12)	(.29)	(.32)	(.15)
	129-138	25-29	13-15	21-25	25-29	65-67
Big Creek Hatchery (7.2)	133.60	27.20	13.53	23.13	25.60	66.07
	(.46)	(.33)	(.13)	(.22)	(.24)	(.21)
	130-136	26-30	13-14	22-25	23-27	65-67
Cowlitz Hatchery stock (7.2)	132.20	26.60	13.60	21.80	26.00	65.67
(Big Creek Hatchery)	(.40)	(.41)	(.13)	(.22)	(.34)	(.16)
	129-135	25-30	13-14	20-23	24-28	65-67
North Nehalem Hatchery (7.7)	130.93	27.73	13.73	23.07	26.13	65.27
	(.42)	(.25)	(.15)	(.27)	(.29)	(.18)
	128-134	26-29	13-15	21-24	24-28	64-66
Trask River Hatchery (9.9)	130.33	25.53	13.67	22.73	25.60	65.40
	(.42)	(.32)	(.13)	(.23)	(.32)	(.24)
	128-133	23-27	13-14	21-24	24-28	63-66
Salmon River Hatchery (7.8)	130.53	26.80	13.67	22.40	26.27	65.53
	(.59)	(.28)	(.16)	(.16)	(.25)	(.19)
	127-135	25-29	13-14	22-24	25-29	64-66
Fall Creek Hatchery (7.4)	131.53	26.20	13.80	22.53	26.07	66.13
(Alsea River)	(.68)	(.33)	(.17)	(.27)	(.23)	(.19)
	127-136	24-28	13-15	21-24	25-28	65-67
Umpqua Hatchery stock (8.6)	129.07	26.40	13.40	21.47	25.87	65.40
(Smith River)	(.37)	(.32)	(.13)	(.17)	(.24)	(.13)
Cole Rivers Hatchery	126-131	24-29	13-14	21-23	24-28	65-66
Cole Rivers Hatchery (8.6)	130.33	26.20	13.80	22.20	26.20	65.20
(Rogue River)	(.66)	(.33)	(.17)	(.30)	(.24)	(.26)
	125-134	24-28	13-15	20-24	25-28	64-67

result of selection, several interacting selective forces were involved.

Life History Characters

Earlier peak spawning times (Table 7) were strongly associated with the northern stream systems and with stream systems having large estuaries (Table 6). However, the correlation of peak spawning time with size of estuary may be biased by the large number of samples from Columbia River hatcheries: spawning times of stocks from the Columbia River are earlier than those of coastal stocks, and the Columbia River has a large estuary. Selection for earlier spawning times through hatchery practices may be the cause for the differences in spawning times between hatchery and wild stocks in the North Nehalem, Trask, and Alsea Rivers. Selection for earlier spawning times has been observed in a steelhead trout hatchery program (Millenbach 1973). At hatcheries using wild stocks as sources for eggs and sperm, peak spawning times were similar to those of naturally spawning fish in the respective stream system.

The proportion of females (Table 7) appeared to be higher in the southern stream systems, suggesting that jacks were more common there. The effective sex ratio, including jacks, at the time of spawning should be close to 1:1 (Fisher 1930). If only 3-yr-old males and females are counted, the proportion of females should be >0.50, the margin above 0.50 depending on how many jacks returned in the previous year. However, the proportion of males was higher than that of females in stocks from the Quilcene, Quinault, Sandy, North Nehalem, Nehalem, Trask, Salmon, Alsea, Umpqua, and Rogue Rivers. Nikolskii (1969) reviewed several possible causes for sex ratios departing from 1:1; however, the reason for the high proportion of males in these stocks is not known.

Isozyme Gene Frequencies

Transferrin gene frequencies (Figs. 2, 3), correlated significantly with six of the stream characters (Table 6). The best model from stepwise multiple regression explained only 68% of the variation in gene frequencies. Analysis of the relationships of the "A" allele frequencies with basin area (Fig. 4) and latitude (Fig. 5) explained the variation more simply than did the stepwise regression model. These correlations showed

TABLE 3.—Means, standard errors (in parentheses), and ranges of morphological characters for 1977 brood year samples of wild juvenile coho salmon. Sample size was 12 for all stream systems except Tenmile Lakes and Coquille River (15 each). The data are listed in north to south order of the sampling locations.

Stream system	Scales in lateral series	Scale rows above lateral core	Anal fin rays	Gill rakers	Branchiostegals	Vertebrae
North Nehalem River	132.25	27.75	13.58	23.25	26.75	65.50
	(.88)	(.33)	(.15)	(.37)	(.25)	(.26)
	126-137	26-30	13-14	22-25	26-28	63-66
Nehalem River	132.50	26.67	13.75	23.00	27.33	65.75
	(.77)	(.35)	(.13)	(.25)	(.22)	(.25)
	127-136	25-29	13-14	22-24	26-28	64-67
Trask River	131.17	26.50	14.00	22.92	26.58	65.83
	(.47)	(.31)	(.12)	(.31)	(.26)	(.11)
	128-133	24-28	13-15	21-24	25-28	65-66
Nestucca River	132.17	26-83	14.00	22.92	27.25	65.58
	(.68)	(.40)	(.12)	(.34)	(.28)	(.19)
	128-136	25-29	13-15	21-25	26-29	65-67
Salmon River	131.83	26.92	13.67	23.08	26.67	65.00
	(.61)	(.31)	(.14)	(.29)	(.19)	(.17)
	128-135	24-28	13-14	22-25	26-28	64-66
Siletz River	130.33	27.08	13.58	23.00	27.50	65.25
	(.61)	(.29)	(.15)	(.21)	(.23)	(.28)
	128-135	26-29	13-14	22-24	26-29	63-67
Beaver Creek	132.27	27.33	13.27	23.27	27.18	65.33
	(.49)	(.38)	(.20)	(.36)	(.30)	(.14)
	130-135	25-29	12.14	21-25	26-29	65-66
Alsea River	131.25	27.17	13.67	23.17	26.83	65.25
	(.37)	(.30)	(.19)	(.34)	(.30)	(.18)
	129-134	26-29	12-14	21-25	26-28	64-66
Umpqua River	131.75	26.83	13.25	22.92	27.00	65.83
	(.70)	(.40)	(.13)	(.19)	(.28)	(.27)
	128-136	25-30	13-14	22-24	26-29	65-68
Tenmile Lakes	131.73	26.20	13.47	22.53	26.60	65.73
	(.58)	(.28)	(.13)	(.19)	(.31)	(.25)
	128-136	25-29	13-14	21-24	25-28	64-67
Coquille River	131.67	26.27	13.27	22.40	26.47	65.93
	(.43)	(.43)	(.18)	(.19)	(.27)	(.21)
	129-134	24-30	13-14	21-24	24-28	65-67
Rogue River	132.75	26.58	14.00	22.50	26.92	65.42
	(.59)	(.26)	(.17)	(.31)	(.40)	(.15)
	131-137	25-28	13-15	21-25	24-29	65-66

TABLE 4.—Hatchery stocks of coho salmon in which differences in morphological characters occurred between the 1976 and 1977 brood years as determined by a two-sample test.

Hatchery	Lateral series scales	Scales above lateral line	Anal rays	Gill rakers	Branchiostegal rays	Vertebrae
Cascade-Bonneville		**				**
Cowlitz stock		**			**	**
Big Creek		**	**			
Trask River	**	**				*
Salmon River					*	
Alsea River		**			*	
Umpqua River	**			*	*	

*$P<0.05$; **$P<0.01$.

that the stocks from large stream systems and the southernmost stream systems had high frequencies of the "A" allele, whereas the frequencies in the smaller stream systems and northern stream systems were highly variable. Combining these two relationships helps explain the pattern of transferrin gene frequencies. Frequencies of the "A" allele were high in stocks from large stream systems regardless of latitude, and in southern stocks regardless of stream size. Stocks from smaller stream systems on the northern Oregon coast and in Washington had higher frequencies of the "C" allele.

The factors affecting the patterns of transferrin gene frequencies in coho salmon stocks are not known. However, Utter et al. (1980) suggested that the frequencies may be influenced by bacteriostatic properties associated with the different transferrin alleles. Genotypes of transferrin had differential mortality when exposed to bacterial kidney disease in studies by Suzumoto et al. (1977) and Winter et al. (1980b), and to vibriosis, cold-water disease, and furunculosis in a study by Pratschner (1978). Transferrin genotype was also related both to differences in juvenile growth rates and to propensity to return as jacks (McIntyre and Johnson 1977).

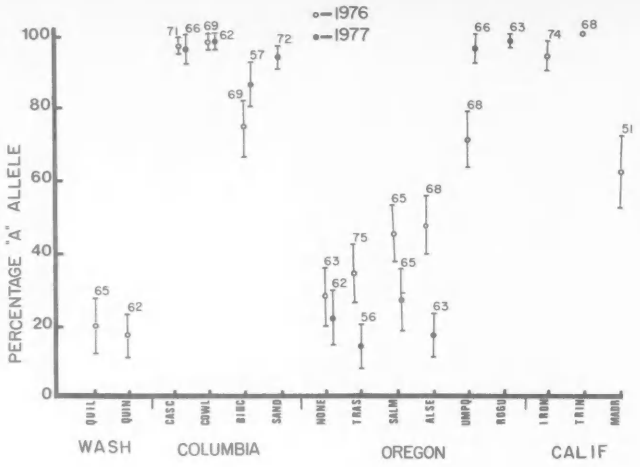

FIGURE 2.—Transferrin gene frequencies of hatchery coho salmon. Samples are arranged from north to south. Vertical lines represent 95% confidence intervals; numbers above the line show sample sizes. Location codes are as in Figure 1.

TABLE 5.—Environmental data for the stream systems sampled in this study.

Stream system	Spawning distance (km)	Latitude	Estuary area (ha)	Estuary length (km)	Gradient (m/km)	Runoff in spring	Basin area (km^2)
Washington							
Quilcene River	13	47.75	[1]512	3.2	19.2	yes	[2]179
Quinault River	92	47.33	[1]64	3.2	2.8	yes	[2]1,123
Oregon							
Columbia River							
Cascade-							
Bonneville Hatcheries	235	46.25	[1]37,513	236.5	0	yes	[3]51,769
Cowlitz Hatchery stock	193	46.25	[1]37,513	109.4	0.8	yes	[2]6,418
Big Creek Hatchery	60	46.25	[1]37,513	43.4	14.2	no	[2]88
Sandy River Hatchery	270	46.25	[1]37,513	194.7	7.1	yes	[2]1,299
North Nehalem River	45	46.25	[4]1,128	11.3	8.6	no	[1]233
Nehalem River	195	45.68	[4]1,128	24.1	2.4	no	[2]2,192
Trask River	72	45.52	[4]3,480	20.9	9.5	no	[5]455
Nestucca River	76	45.16	[4]400	12.9	7.7	no	[2]657
Salmon River	29	45.05	[4]82	6.4	13.0	no	[6]194
Siletz River	122	44.93	[4]475	37.0	3.4	no	[2]797
Beaver Creek	21	44.52	[1]3	3.2	4.3	no	[1]31
Alsea River	93	44.43	[4]858	19.3	3.2	no	[6]1,227
Umpqua River	372	43.68	[4]2,285	45.0	1.9	yes	[6]11,801
Smith River[7]	122	43.68	[4]2,285	24.1	2.5	no	[2]898
Tenmile Lakes	24	43.57	[1]1	1.6	3.2	no	[5]254
Coquille River	138	43.11	[4]308	66.0	3.4	no	[6]2,738
Rogue River	249	42.44	[4]251	6.4	1.9	yes	[6]13,199
California							
Klamath River	293	41.58	[1]200	3.2	2.2	yes	[8]31,314
Trinity River	235	41.58	[1]200	3.2	2.4	yes	[8]7,383
Mad River	72	40.95	[1]200	6.4	6.5	no	[8]1,255

[1]Provided by district biologists.
[2]Pacific Northwest River Basins Commission. 1966, 1967, 1968, 1969, 1972. River Mile Indices. Hydrol. Hydraul. Comm.
[3]Personal estimate of area utilized by coho in the Columbia drainage.
[4]Gaumer, T., D. Demory, and L. Osis. 1973. Estuary resources use study. Fish Comm. Oreg., Div. Manage. Res.
[5]Water Resources Board of Oregon. 1969. Oregon long range requirements for water. Salem, Oreg., 397 p.
[6]Wilsey and Ham Incorp. 1974. Estuarine resources of the Oregon coast. A natural resource inventory report to the Oregon Coastal Conservation and Development Commission, Portland, Oreg., 233 p.
[7]Source of Umpqua Hatchery stock.
[8]United States Geological Survey. 1977. Water resources data for California water year 1977. Water Data Rep. CA 77-2.

Therefore, diseases, life history characteristics, and other factors may play a role in maintaining the patterns of transferrin gene frequencies.

Transferrin gene frequencies were in good agreement between the two year classes of Oregon coast wild stocks, despite the small size of some of the samples (Fig. 3). The heterogeneity between year classes was greater for the Oregon

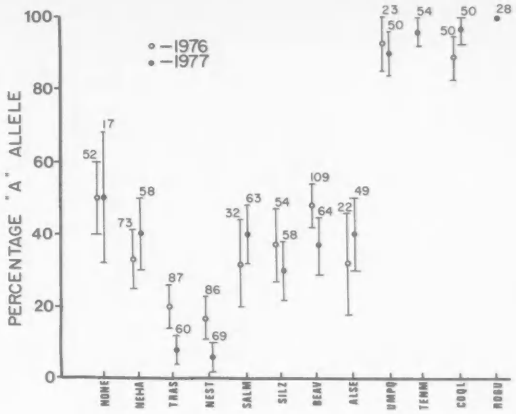

FIGURE 3.—Transferrin gene frequencies of wild coho salmon stocks for 1976 and 1977 brood years. Stocks are arranged from north to south. Bars represent 95% confidence intervals and the sample sizes are above the bars. Location codes are as in Figure 1.

TABLE 6.—Statistically significant correlation coefficients between the characteristics of the coho salmon stocks and the environmental characteristics of their respective stream systems. $r = 0.28$ at $\alpha = 0.05$ and 0.37 at $\alpha = 0.01$.

Characteristics		
Stock	Environmental	Correlation
Scales in lateral series	Spawning distance	0.418
	Estuary size	0.341
	Estuary length	0.430
	Gradient	−0.368
Scale rows	Latitude	0.360
	Spring runoff	0.315
Anal rays	Estuary size	0.414
	Latitude	0.382
Gill rakers	Latitude	0.346
	Basin area	−0.353
	Spring runoff	−0.319
Branchiostegals	Latitude	0.431
	Spring runoff	0.381
Vertebrae	Estuary size	0.350
	Basin area	0.445
	Gradient	−0.432
	Spawning distance	0.549
	Estuary length	0.533
Proportion of females	Latitude	−0.426
Time of peak spawning	Estuary size	−0.613
	Spring runoff	−0.345
	Estuary length	−0.391
	Latitude	−0.702
Phosphoglucose isomerase	Spring runoff	−0.410
Transferrin	Estuary length	0.326
	Latitude	−0.381
	Spawning distance	0.590
	Basin area	0.588
	Spring runoff	0.528
	Gradient	−0.596

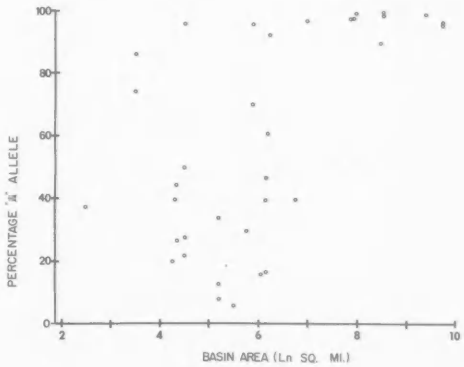

FIGURE 4.—Transferrin gene frequencies for wild and hatchery coho salmon stocks arranged by basin area, in ln square miles.

coast hatchery stocks (Fig. 2). The gene frequencies of hatchery stocks may have been altered by earlier importing of stocks with different gene frequencies, or by disease epizootics. If fish with certain transferrin genotypes have different resistances to diseases, and if epizootics are more severe because of the higher densities of fish in hatcheries, then the transferrin gene frequency of a given year class could be altered without affecting the other two year classes.

The phosphoglucose isomerase variant (Table 7) was present only in samples from Oregon stocks—particularly those from the northern Oregon coast. May (1975) reported this variant in Washington stocks.

Similarity of Stocks

The groups of stocks of coho salmon found to be most similar by the agglomerative cluster analysis (Fig. 6) were composed of northern

TABLE 7.—Proportion of females, time of peak spawning, and gene frequency, 95% confidence interval (CI), and sample size of phosphoglucose isomerase variant of wild and hatchery stocks of coho salmon. Years of data used to estimate proportion of females are in parentheses. The data are listed in north to south order of the sampling locations.

Stream system	Proportion of females[1]	Years	Time of peak spawing[1]	Proportion of females	Years	Time of peak spawning[1]	1977			1976			1977		
							Frequency	95% CI	Sample size	Frequency	95% CI	Sample size	Frequency	95% CI	Sample size
Washington:															
Quilcene Hatchery				0.41	1972-78	Oct. 15-30				0	—	36			
Quinault Hatchery				0.37	1973-75	Oct. 15-30				0	—	40			
Oregon:															
Columbia River					—										
Cascade-Bonneville Hatchery				0.51	1970,72-76	Nov. 1 -15				0	—	40	0	—	60
Cowlitz Hatchery stock				0.50	([2])	Nov. 1 -15				0	—	40	0	—	60
Big Creek Hatchery				0.55	1970-76	Nov. 1 -15				0	—	40	0	—	40
Sandy River Hatchery				0.45	1970-76	Nov. 1 -15				0	—	40			
North Nehalem River	0.43	([3])	Dec. 1 -15	0.43	1970-76	Nov. 1 -15	0.05	0.08	19	0.05	0.04	44	0.08	0.04	60
Nehalem River	0.43	1949-69	Dec. 1 -15				0.11	0.06	64						
Trask River	0.33	1949-69	Dec. 1 -15	0.43	1970-76	Nov. 1 -15	0.06	0.04	62	0.08	0.06	40	0.20	0.08	60
Nestucca River	0.56	1949-69	Dec. 1 -15				0.03	0.04	59						
Salmon River	0.46	1975-77	Dec. 1 -15	0.46	1975-77	Dec. 1 -15	0.01	0.02	64	0	—	40	0	—	60
Siletz River	0.54	1949-69	Dec. 1 -15												
Beaver Creek	0.58	1949-69	Dec. 15-31				0	—	32						
Alsea River	0.53	1949-69	Dec. 1 -15	0.42	1970-76	Nov. 16-30	0.01	0.02	49	0.05	0.04	40	0.15	0.06	60
Umpqua River	0.63	1949-69	Dec. 1 -15	0.49	1977-78	Dec. 1 -15	0	—	41	0	—	40	0		60
Tenmile Lake	0.65	[4]1954-74	Dec. 15-31				0	—	50						
Coquille River	0.55	1949-69	Dec. 1 -15				0.01	—	59						
Rogue River	0.44	([3])	Dec. 1 -15	0.44	1974,75, 77 & 78	Dec. 1 -15	0	—	29				0		60
California:															
Klamath River															
Irongate Hatchery				0.53	1969-78	Dec. 1 -15				0		40			
Trinity Hatchery				0.53	1966-78	Dec. 1 -15				0		40			
Mad River				0.62	1971-78	Dec. 1 -15				0		36			

[1]Three-year-old fish only.
[2]Estimated by hatchery manager.
[3]Estimated from hatchery data.
[4]Except 1959.

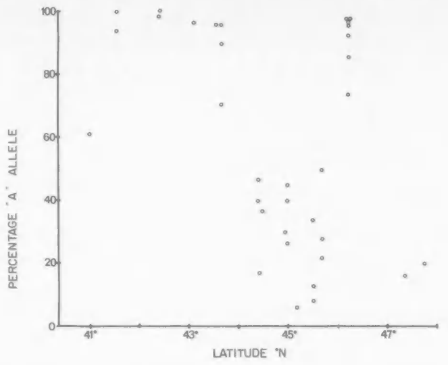

FIGURE 5.—Transferrin gene frequencies for wild and hatchery coho salmon stocks arranged by latitudes.

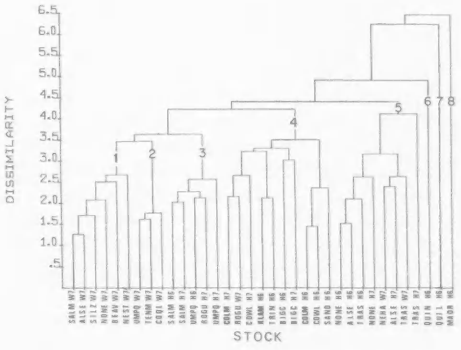

FIGURE 6.—Dendrogram of the agglomerative cluster analysis for all stocks of wild and hatchery coho salmon of two brood years, 1976 and 1977. Euclidean distance was the dissimilarity measure and group average was the clustering strategy. Location codes are as in Figure 1. The other codes are as follows: H6, hatchery stock of the 1976 brood year; H7, hatchery stock of the 1977 brood year; and W7, wild stock from the 1977 brood year.

Oregon coast wild stocks (cluster 1), southern Oregon coast wild stocks (cluster 2), stocks from hatcheries that used wild stocks for the egg source (cluster 3), stocks from large river systems (cluster 4), hatchery stocks and two wild stocks from the northern Oregon coast (cluster 5), and three individual hatchery stocks from California and Washington (clusters 6-8).

Canonical variate analysis on the five larger clusters produced three canonical variables that were significant ($\alpha = 0.05$). When these three variables were plotted against each other, only clusters 1 and 5 (consisting of wild stocks and hatchery stocks, both from the northern Oregon coast) were not completely separate in three-dimensional space. The other three clusters were discrete, suggesting that intercluster differences were stronger than between clusters 1 and 5. Statistical testing for differences between the clusters would not be valid because the necessary assumption of randomness of data is violated.

The results of the canonical variate analysis must be interpreted with caution because the variation within each cluster was reduced by our using the averages of the morphological characters. This reduction of variation facilitates discrimination between clusters by canonical variate analysis, so that quantitative comparisons of cluster discreteness cannot be made. Individual phenotypes undoubtedly overlap between stocks or between clusters; however, the multivariate analysis of variance did indicate that significant differences existed among the stocks for each of the morphological characters. We characterized the stocks by the average phenotypes in order to estimate the phenotypes typical for each stream system, and on that basis the results of the canonical variate analysis suggested that there were discrete differences between all clusters except 1 and 5.

The results of the agglomerative and divisive cluster analyses were similar. At the 13-cluster level of the divisive analysis (Table 8), all but two clusters were identical with clusters from the agglomerative cluster analysis dendrogram. The results of these analyses should be interpreted cautiously, because they are based on only 10 characteristics—a small number compared with the total number of genetically related characteristics possible. If other characteristics had been used, the results might have differed. Thus, we did not emphasize the exact order or the levels of dissimilarity at which any two clusters joined together; rather, we observed only general trends in the clustering patterns.

Three general trends are apparent in the clustering patterns of the agglomerative cluster analysis dendrogram. First, the stocks from the larger stream systems (Columbia, Rogue, and Klamath Rivers) were more similar to each other than to the stocks from smaller streams. The only exceptions to this trend were wild stock from the Umpqua River and the Umpqua and Rogue hatchery stocks. The Umpqua wild stock was

TABLE 8.—Coho salmon stocks at the 13 cluster level of the divisive cluster analysis. "Wild" denotes wild stocks.

Cluster no.	Divisive cluster analysis stock	Brood year
1	Cascade Hatchery	1976
	Cowlitz Hatchery	1976
	Sandy Hatchery	1976
2	Salmon River Hatchery	1976, 1977
	Rogue River Hatchery	1977
	Umpqua River Hatchery	1976, 1977
3	North Nehalem wild	1977
	Nestucca River wild	1977
	Salmon River wild	1977
	Siletz River wild	1977
	Beaver Creek wild	1977
	Alsea River wild	1977
4	Quilcene Hatchery	1976
5	Nehalem River wild	1977
	Trask River wild	1977
6	Mad River Hatchery	1976
7	North Nehalem Hatchery	1976, 1977
	Trask Hatchery	1976
	Alsea Hatchery	1976
8	Umpqua River wild	1977
	Tenmile Lake wild	1977
	Coquille River wild	1977
9	Trask Hatchery	1977
	Alsea Hatchery	1977
10	Quinault Hatchery	1977
11	Bonneville Hatchery	1977
	Cowlitz Hatchery	1977
	Rogue wild stock	1977
12	Irongate Hatchery	1976
	Trinity Hatchery	1976
13	Big Creek Hatchery	1976, 1977

associated with the other southern Oregon coast wild stocks, and the Rogue and Umpqua hatchery stocks were in the cluster with other hatcheries that used wild stocks as egg sources.

The second trend observed in the dendrogram was geographical clustering. Three stocks from Washington and California were dissimilar to the Oregon stocks, and the Oregon wild stocks clustered into two groups, northern and southern coastal stocks.

The third trend in the dendrogram was for hatchery and wild stocks to cluster independently. One of the clusters was composed entirely of wild stocks from the northern Oregon coast, and another included all but one of the northern Oregon coast hatchery stocks, in addition to two wild stocks from the northern Oregon coast. The hatchery stock excluded from this cluster (no. 5) was from the Salmon River, a stock developed from eggs of wild coho salmon; both brood years of this stock were in the cluster of hatcheries that used wild stocks as an egg source. The rest of the northern Oregon coast hatcheries used returning hatchery-reared adults for egg sources. The two wild stocks in this cluster were from the Trask and Nehalem Rivers. They are also similar to the other wild stocks; however, because of the mechanics of the group-average clustering strategy, they both clustered first with the hatchery stocks. The average Euclidean distance between the Nehalem wild stock and the other wild stocks was less than that between the Nehalem wild stock and the hatchery stocks of cluster 5. The close relationships of the stocks in clusters 1 and 5 were also apparent in the results of the canonical variate analysis, which showed these two clusters to be continuous.

The three trends in the clustering pattern indicated that coho salmon stocks from similar environments had similar phenotypes. These trends provide some guidance for the transfer of coho salmon stocks. Geographical clustering indicates that the phenotypic or perhaps genetic similarity between stocks probably decreases as the distance between stocks increases. McIntyre[8] showed a strong negative correlation for the distance between stream systems and the genetic similarity of the steelhead trout stocks in those stream systems. If a similar relation between phenotype and distance exists among coho salmon stocks, survival rate would be expected to vary inversely with the distance that the stock is transferred from its native stream. The crucial question from the management standpoint, assuming the relationships we found are real, is how far stocks can be transferred before decreasing survival rate and the increasing genetic impact on the native stocks reduce the practicality of such transfers.

Although geographical distance can be an important factor in selecting a donor stock, other considerations must also be taken into account. The difference between stocks from large and small stream systems illustrates a problem in basing stock transfers primarily on geographical distance. Stocks from large stream systems were more similar to stocks in distant large systems than to stocks in small stream systems that were geographically close. Other environmental variables may also differ, affecting the phenotypes of geographically close stocks. Characteristics such as time of peak spawning or transferrin genotype may be closely related to flow and temperature regimes or to disease organisms present in the stream systems. These characteristics and others not included in this

[8]McIntyre, J. D. 1976. The report of interbreeding of artificially propagated and native stocks of steelhead trout. Oreg. Dep. Fish Wildl., Res. Sect., Steelhead Annu. Rep., 22 p.

study all should play a role in choosing stocks for transfer to other stream systems.

The third trend mentioned (that of hatchery and wild stocks diverging toward different phenotypes) presents a problem to managers who must choose the best stock for transfer to other stream systems. The separate clustering of hatchery and wild stocks suggests that hatchery stocks have become dissimilar to wild stocks—even those that inhabit the same drainage. Studies with steelhead trout indicated that hatchery fish survived better in hatchery ponds, whereas wild fish had higher survival in streams (Reisenbichler and McIntyre 1977). The dissimilarity between hatchery and wild stocks may play a role in reducing the survival of hatchery-reared coho salmon when they are released into a stream system.

Similarity of Stream Systems and Wild Stocks

Because coho salmon appear to have similar phenotypes in similar environments, one could possibly relate phenotypes of stocks with descriptions of their stream basins (Tables 5, 9). However, comparisons of an agglomerative cluster analysis of wild stocks (Fig. 7) with a cluster analysis of stream characters (Fig. 8) indicated that they were less similar than we had anticipated—although we expected some differences because the stream characters were not necessarily related to taxonomic characters used in this study.

CONCLUSIONS

Individual characters of the stocks examined by us showed a variety of responses to stream characters. Time of peak spawning was strongly correlated with latitude, whereas other characters were significantly correlated with several environmental gradients, suggesting that interactions determining stock phenotypes are complex. The variability of the stock character may also change along environmental gradients, as demonstrated by the transferrin genotype (Figs. 4, 5).

The results of the cluster analysis indicate that stocks that are geographically close are similar, that stocks from large stream systems are similar to each other, that stocks from coastal stream systems are similar to each other, and that hatch-

TABLE 9.—Fish species and myxosporidan parasite, *Ceratamyxa shasta*, present in the Oregon stream systems. X = present.

Stream systems	Carp	Oregon chub	Squawfish	Redside shiner	*Catostomus* sp.	Speckled dace	Striped bass	Brown bullhead	Largemouth bass	*Ceratamyxa shasta*
Nehalem River					X				X	X
Trask River										
Nestucca River						X				
Salmon River										
Siletz River						X		X		
Beaver Creek						X				
Alsea River						X				
Smith River		X	X	X	X		X	X		
Umpqua River		X	X	X	X	X	X	X		
Tenmile Lake						X		X	X	
Coquille River					X	X	X	X		
Rogue River	X			X	X		X	X		X

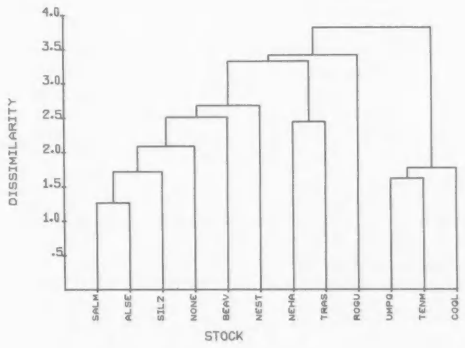

FIGURE 7.—Dendrogram of the agglomerative cluster analysis for wild coho salmon stocks with a Euclidean distance dissimilarity measure and group average clustering strategy. Location codes are as in Figure 1.

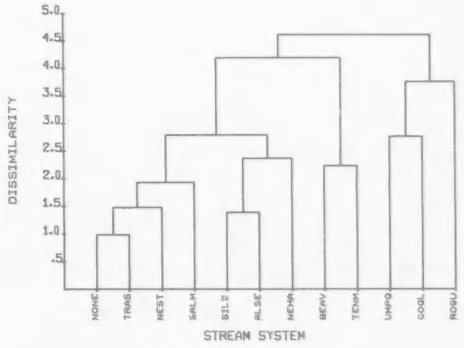

FIGURE 8.—Dendrogram of the agglomerative cluster analysis for stream systems with a Euclidean distance measure and group average clustering strategy. Location codes are as in Figure 1.

ery and wild stocks are dissimilar. In general, coho salmon stocks from similar environments appear to have similar phenotypes; however, groupings obtained from cluster analyses of coho salmon stocks and corresponding stream systems were dissimilar. This dissimilarity may be a result of our using only a small number of characters for analysis. As additional characters are considered, additional trends may become evident. The characters in this study, in concert with other characters, should be used in future evaluations of genetic similarities between stocks for an eventual characterization of stocks that will ensure effective transplantation.

In addition to providing information which may be useful for selecting donor stocks for hatchery programs, the results of this study also suggest a potential weakness in hatchery supplementation. Selection through hatchery environment and hatchery practices may be changing the overall phenotype of hatchery stocks, as well as the between-year variability of individual genotypes (as we found for transferrin). If these changes result in reduced performance of the donor stocks in other stream systems, practices designed to increase hatchery production must be weighed against the actual benefits to wild production.

We believe that this study demonstrates a relationship between phenotypic characters and certain habitat types. The differences in phenotype that are attributable to hatchery or wild origin, geographic proximity, and small or large stream systems may provide a first basis for judging the advisability of stock transfers.

ACKNOWLEDGMENTS

We express our appreciation to Carl Bond for his suggestions concerning the morphological characters, to Norbert Hartmann for his advice concerning the analysis of the data, to Fred Utter for taking the time to share his knowledge of electrophoresis, and to Al McGie for providing data on the proportion of females on spawning ground surveys. Funds for this project were provided by the Oregon Department of Fish and Wildlife.

LITERATURE CITED

BAMS, R. A.
1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Board Can. 33:2716-2725.

BARLOW, G. W.
1961. Causes and significance of morphological variation in fishes. Syst. Zool. 10:105-117.

BLACKITH, R. E., AND R. A. REYMENT.
1971. Multivariate morphometrics. Acad. Press, Lond., 412 p.

CLIFFORD, H. T., AND W. STEPHENSON.
1975. An introduction to numerical classification. Acad. Press, N.Y., 229 p.

FELDMANN, C. L.
1974. The effect of accelerated growth and early release on the timing, size and number of returns of coho salmon (*Oncorhynchus kisutch*). M.S. Thesis, Univ. Washington, Seattle, 46 p.

FISHER, R. A.
1930. The genetical theory of natural selection. Oxf. Univ. Press. (Clarendon), Lond., 272 p.

HARRELL, L. W., A. J. NOVOTNY, M. H. SCHIEWE, AND H. O. HODGINS.
1976. Isolation and description of two vibrios pathogenic to Pacific salmon in Puget Sound, Washington. Fish. Bull., U.S. 74:447-449.

MACGREGOR, R. B., AND H. R. MACCRIMMON.
1977. Evidence of genetic and environmental influences on meristic variation in the rainbow trout, *Salmo gairdneri* Richardson. Environ. Biol. Fishes 2:25-33.

MAY, B.
1975. Electrophoretic variation in the genus *Oncorhynchus*: The methodology, genetic basis, and practical applications to fisheries research and management. M.S. Thesis, Univ. Washington, Seattle, 95 p.

MCINTIRE, C. D.
1973. Diatom associations in Yaquina Estuary, Oregon: a multivariate analysis. J. Phycol. 9:254-259.

MCINTYRE, J. D., AND A. K. JOHNSON.
1977. Relative yield of two transferrin phenotypes of coho salmon. Prog. Fish-Cult. 39:175-177.

MILLENBACH, C.
1973. Genetic selection of steelhead trout for management purposes. *In* M. W. Smith and W. M. Carter (editors), International Atlantic salmon symposium, p. 253-257. Int. Atl. Salmon Found., N.Y.

MYERS, K. W.
1979. Comparative analysis of stomach contents of cultured and wild juvenile salmonids in Yaquina Bay, Oregon. *In* S. J. Lipovsky and C. A. Simenstad (editors), Fish food habits and studies, Proceedings of the Second Pacific Northwest Technical Workshop, p. 155-162. Wash. Sea Grant Publ., Univ. Washington, Seattle.

NEAVE, F.
1944. Racial characteristics and migratory habits in *Salmo gairdneri*. J. Fish. Res. Board Can. 6:245-251.

NIKOLSKII, G. V.
1969. Theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources. Oliver and Boyd, Edinb., 323 p.

PRATSCHNER, G. A.
1978. The relative resistance of six transferrin phenotypes of coho salmon (*Oncorhynchus kisutch*) to cytophagosis, furunculosis, and vibriosis. M.S. Thesis, Univ. Washington, Seattle, 71 p.

RAO, C. R.
1970. Advanced statistical methods in biometric research. Hafner Publ. Co., Darien, Conn., 390 p.

REISENBICHLER, R. R., AND J. D. MCINTYRE.
1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 34:123-128.

RICKER, W. E.
1970. Hereditary and environmental factors affecting certain salmonid populations. *In* R. C. Simon and P. A. Larkin (editors), The stock concept of Pacific salmon, p. 19-160. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

RIDGWAY, G. J., S. W. SHERBURNE, AND R. D. LEWIS.
1970. Polymorphism in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99:147-151.

ROLEY, D. D.
1973. An evaluation of the selective breeding of steelhead trout (*Salmo gairdneri gairdneri*) and coho salmon (*Oncorhynchus kisutch*) at Eagle Creek National Fish Hatchery, Oregon. M.S. Thesis, Univ. Washington, Seattle, 198 p.

SIMON, R. C., AND P. A. LARKIN (editors).
1970. The stock concept of Pacific salmon. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, 231 p.

SMITH, S. B.
1969. Reproductive isolation in summer and winter races of steelhead trout. *In* T. G. Northcote (editor), Symposium on salmon and trout in streams, p. 21-38. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

SNEATH, P. H. A., AND R. R. SOKOL.
1973. Numerical taxonomy, the principles and practice of numerical classification. W. H. Freeman, San Franc., 573 p.

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

SUZUMOTO, B. K., C. B. SCHRECK, AND J. D. MCINTYRE.
1977. Relative resistance of three transferrin genotypes of coho salmon (*Oncorhynchus kisutch*) and their hematological responses to bacterial kidney disease. J. Fish. Res. Board Can. 34:1-8.

TÅNING, A. V.
1952. Experimental study of meristic characters in fishes. Biol. Rev. (Camb.) 27:169-193.

UTTER, F. M., W. E. AMES, AND H. O. HODGINS.
1970. Transferrin polymorphism in coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 27:2371-2373.

UTTER, F. M., D. CAMPTON, S. GRANT, G. MILNER, J. SEEB, AND L. WISHARD.
1980. Population structures of indigenous salmonid species of the Pacific Northwest. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific, p. 285-304. Oreg. State Univ. Press, Corvallis.

WINTER, G. W., C. B. SCHRECK, AND J. D. MCINTYRE.
1980a. Meristic comparison of four stocks of steelhead trout (*Salmo gairdneri*). Copeia 1980:160-162.
1980b. Resistance of different stocks and transferrin genotypes of coho salmon, *Oncorhynchus kisutch*, and steelhead trout, *Salmo gairdneri*, to bacterial kidney disease and vibriosis. Fish. Bull., U. S. 77:795-802.

REPRODUCTIVE BIOLOGY OF WESTERN ATLANTIC BLUEFIN TUNA[1]

RAYMOND E. BAGLIN, JR.[2]

ABSTRACT

Ovaries of bluefin tuna, *Thunnus thynnus*, were collected from the Gulf of Mexico, Florida Straits, Middle Atlantic Bight of the western North Atlantic, and off the northeast coast of the United States. There was relatively little development towards maturity in age 1 through age 7 fish from the Middle Atlantic Bight as evidenced by low gonosomatic index values and histological examination of ovaries. Well-developed ovaries were present in giant bluefin tuna from the Gulf of Mexico and Florida Straits, with heaviest spawning occurring in May. For bluefin tuna measuring 205-269 cm fork length and 156-324 kg round weight, the average number of eggs measuring 0.33 mm in diameter and larger was estimated at 60.3 million, and the average number of eggs measuring 0.47 mm in diameter and larger was estimated at 34.2 million.

Atlantic bluefin tuna, *Thunnus thynnus*, are seasonally distributed over most of the North Atlantic. They are found from Newfoundland to Brazil and from Norway to the Canary Islands (Gibbs and Collette 1967).

In the western Atlantic, a sport fishery for bluefin tuna exists off the east coast of the United States from Maine through North Carolina and along the western Bahamas and the eastern coast of Canada. Also, a substantial commercial bluefin tuna fishery exists in the western Atlantic. There is purse seining along the east coast of the United States from Massachusetts to North Carolina and a handline and harpoon fishery off Massachusetts and Maine. A substantial Japanese longline fishery is present off the east coast of the United States and in the Gulf of Mexico.

In the eastern Atlantic, a sport fishery for bluefin tuna exists around the Canary Islands and a substantial commercial fishery occurs off Europe and North Africa. Purse seining is conducted off the Atlantic coast of Norway and Morocco, the Mediterranean coast of France, the Adriatic coast of Italy and Yugoslavia, in the Tyrrhenian Sea off Italy, and occasionally in the North Sea off Denmark. An important hook-and-line bait fishery occurs in the Bay of Biscay off France and Spain, off Morocco, the Azores, the Canary Islands, the Mediterranean coast of Spain, and occasionally off Turkey. Trap fisheries were present off southern Portugal, southern Spain, and the Straits of Gibraltar, as well as along the Mediterranean coast of Morocco, Tunisia, and Sicily. There is a significant Japanese longline bluefin tuna fishery in the Mediterranean Sea, Bay of Biscay, and off western Europe.

There has been a substantial reduction in the Atlantic-wide catch of bluefin tuna from 38,500 t in 1964 to 12,500 t in 1973 with no large reductions in effort (Miyake et al[3].) A number of studies have been made, and are continuing, to understand the reason for this decline (Parks 1977; Shingu and Hisada 1980; Parrack 1980). Of the various aspects of the dynamics of fish populations, the measure of reproductive potential is of primary importance since it is a basic determinant of productivity. It is used to separate subpopulations, to estimate mortality, and, with ichthyoplankton data, to estimate stock size.

Two major bluefin tuna spawning areas are located in the Atlantic approximately 4,000 mi apart: In the Gulf of Mexico (Richards 1976; Montolio and Juarez 1977; Rivas 1978) and the Florida Straits (Rivas 1954; Baglin 1976) during April, May, and June; and in the Mediterranean Sea during May, June, and July (Frade and Manaças 1933; Rodrîguez-Roda 1964). Al-

[1]Contribution Number 81-34 M, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, Miami, FL 33149.

[2]National Marine Fisheries Service, NOAA, c/o Alaska Department of Fish and Game, P.O. Box 686, Kodiak, AK 99615.

[3]Miyake, M. P., A. De Boisset, and S. Manning (compilers). 1974. Int. Comm. Conserv. Atl. Tunas, Stat. Bull. 5. Unnumbered pages.

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though these two spawning grounds have been well documented, a question remains whether bluefin tuna spawn elsewhere and at other times. Mather[4] believes that some bluefin tuna probably spawn in late spring near the northern edge of the Gulf Stream off the eastern United States. Berrien et al. (1978) have reported collecting bluefin tuna larvae from this area during April and June 1966. These larvae, however, could have drifted to this area from spawning grounds farther south.

In this paper, I describe bluefin tuna ovaries from the Middle Atlantic Bight (the U.S. coastal area between Cape Cod and Cape Hatteras) and examine the possibility that this may be another significant spawning area for bluefin tuna. Also, I make some comparisons of female gonadal development between the known spawning areas.

My literature review on bluefin tuna shows there is a need for additional information on the bluefin tuna's reproductive potential. A wide range in fecundity estimates was found. Frade (1950) reported that an eastern Atlantic 160 kg bluefin tuna produced 18.7 million eggs. Williamson (1962) stated that the ovaries of a 272.4 kg western Atlantic bluefin tuna contained about 1.0 million eggs. Rodríguez-Roda (1967) estimated that off southern Spain a 54 kg fish could produce 5.5 million eggs and a 235 kg bluefin tuna could produce over 30.0 million eggs. Baglin (1976) estimated that a 188.4 kg western Atlantic bluefin tuna could produce 16.7 million eggs and that a 271.5 kg bluefin tuna could produce 31.4 million eggs. Baglin and Rivas (1977) indicated that a 324 kg western Atlantic tuna could produce 57.6 million eggs. I determined the fecundity of bluefin tuna taken from the United States sport fishery in the Florida Straits and Gulf of Mexico and from the Japanese longline fishery in the Gulf of Mexico and compared my findings with previous estimates. I have also examined monthly sex ratios for western Atlantic bluefin tuna.

MATERIALS AND METHODS

Bluefin tuna from the Gulf of Mexico, Florida Straits, Middle Atlantic Bight, and off the northeast coast of the United States were sampled from anglers' catches. Bluefin tuna samples from purse seine catches came from the Middle Atlantic Bight and the northeast coast of the United States. Bluefin tuna were also sampled from the Japanese longline fishery in the Gulf of Mexico and from the New England handgear fishery.

Throughout this paper the classification system of Rivas (1979) was used. Thus, small bluefin tuna are 50-129 cm fork length (FL) and 3-44 kg round weight, medium bluefin tuna are 130-180 cm FL and 45-130 kg round weight, and giant bluefin tuna are >180 cm FL and >130 kg round weight.

Sex data were obtained from 283 small and medium bluefin tuna captured by commercial and sport fishermen off the Middle Atlantic Bight (1974-77). Also, sex data were obtained from 3,429 giant bluefin tuna captured by sport and commercial fishermen in the Gulf of Mexico and along the northeast coast of the United States from North Carolina to Maine, and from fish taken by sport fishermen in the Bahamas (1975-78).

Straight fork length (cm) was measured with calipers and round weight was recorded in pounds and later converted to kilograms. In some instances where either weight or length was unknown, a functional regression (Baglin 1980) was used for estimating the missing measurement.

Small and medium fish were assigned an age based on a length-weight-age conversion table presented by Coan (1976). No ages were assigned to giant fish because of the difficulty experienced in aging them accurately.

Ovaries were examined from 81 small and medium bluefin tuna caught from 1974 through 1977 and from 403 giant bluefin tuna collected during 1965 through 1968 and 1974 through 1978. Ovaries were stored in 10% Formalin[5] and later blotted dry and weighed in grams. The gonosomatic index (GSI) (ovary weight as a percentage of total body weight) was used as a gross indicator of maturity. Only fork length was taken from Japanese longline samples from the Gulf of Mexico for which the GSI was calculated using an estimated body weight from the length-weight relationship of Baglin (1980).

A detailed examination of ovaries from 292

[4]Mather, F. J., III. 1973. The bluefin tuna situation. Proc. 16th Annu. Int. Game Fish. Res. Conf., p. 93-120.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

fish was conducted using histological techniques. Ovaries were sectioned at 8 μ and stained either with haematoxylin and eosin or trichrome stain. The oocytes were grouped into stages according to the classification system of Kraft and Peters (1963) and Smith (1965). From each prepared slide, a measurement was taken of the largest egg diameter. The egg diameters were measured with an ocular micrometer at 30 × magnification, and the orientation of egg diameters was assumed to be random. Stage of maturity was thus based on the histological examinations.

A test was made for heterogeneity of egg size within the ovary. Thin cross sections were taken from the anterior, middle, and posterior parts of one ovary of a mature fish and each section was subdivided into three subsamples, representing the center, midregion, and periphery of the ovary (Otsu and Uchida 1959). Egg diameters from each area were then measured and compared statistically.

Fecundity, defined as the potential number of mature eggs (yolked ova) that could be spawned during one reproductive season, was estimated by using a dry weight method. This consisted of taking samples from the anterior, middle, and posterior parts of each ovary. The eggs from each of these sections and from the remainder of the ovaries were then separated from the ovarian tissue by straining them over a wire screen under running water. The egg samples from each section, in an aqueous solution, were stirred and a subsample from each was pipetted into a beaker. These eggs were stirred and approximately 1-2 g wet weight were taken to be used for the fecundity estimate. The yolked eggs, which were counted and fecundity estimated, were divided into two size categories. Eggs 0.46 mm and larger that were counted were well developed and fully yolked. A second size category for which eggs were counted included smaller eggs (0.32 mm in diameter) that were not in quite as advanced stage of development, but that could possibly undergo further development and be spawned during one reproductive season. The subsample was then weighed to the nearest 0.1 mg, and the weight of the remaining eggs was recorded in grams. Fecundity estimates, rounded to the nearest 0.1 million eggs, were calculated from the relationship $C = (AD/B) + A$, where A is the number of mature ova in the subsample, B is the weight of the ova in the subsample, C is the number of mature ova, and D is the weight of ova from both ovaries minus the weight of the subsample.

RESULTS AND DISCUSSION

Sex Composition

From 1974 through 1977, sex was determined for 283 small and medium bluefin tuna from the Middle Atlantic Bight during June, July, and August (Table 1). No significant difference from an expected 1:1 sex ratio was found. Sampling for the remaining months was inadequate.

From 1975 through 1978, sex was determined for 3,429 giant bluefin tuna from the Gulf of Mexico, March through June; Bahamas, April through June; and from the northeast coast of the United States, July through October (Table 1). The deviation from an expected 1:1 sex ratio was significant for April, May, July, and August. Females were more prevalent than males in spawning aggregations during April and May. Males were more prevalent in feeding schools during July and August. No significant difference from an expected 1:1 sex ratio was found for March, June, September, and October. Sampling during the remaining months was inadequate. These findings suggest that some giant bluefin tuna segregate into distinct areal groups according to the predominating sex and that sex ratios may change with season.

TABLE 1.—Monthly sex ratios for small and medium (1974-77) and giant (1975-78) western Atlantic bluefin tuna.

Size category	Month	Number	Sex ratio males/females
Small and medium	June	204	1.02
	July	35	0.84
	August	44	1.10
Giant	March	65	1.00
	April	292	[1]0.75
	May	356	[1]0.63
	June	106	0.93
	July	800	[1]1.46
	August	1,049	[1]1.74
	September	694	0.93
	October	66	1.13

[1]Significant departure from null hypothesis at 0.05 level (chi-square).

Gonosomatic Index, Gross Morphology, and Size of Ova

The external appearance alone of tuna ovaries is inadequate for gross classification of maturity stage (Buñag 1956). The GSI (also called gonad index, maturity index, gonadosomic or gonadal-

somatic index), along with egg diameter measurements, has been a successfully used criterion for selecting specimens for fecundity studies and for determining the spawning periods for various species of fish (Vladykov 1956; Peterson 1961; Erdman, 1968; Mathur and Ramsey 1974; Baglin 1979).

On the basis of the GSI and the gross morphology and size of ova from the preserved ovaries, western Atlantic female bluefin tuna may be assigned to one of the following developmental stages:

I. Immature—Ovaries are thin, hollow tubes; nearly spherical, transparent oocytes range from 0.03 to 0.13 mm in diameter (these eggs were stained with acetocarmine to facilitate measuring). These oocytes were also present during all other developmental stages, and there was no sign of previous spawning. GSI ranges from 0.1 to 0.3.

II. Maturing—Ovaries are flaccid, opaque ova up to about 0.63 mm in diameter. GSI ranges from 0.4 to 1.9.

III. Mature—Ovaries are firm and full of eggs, with many yellow-orange ova up to 0.85 mm in diameter. GSI ranges from 2.0 to 5.3.

IV. Ripe—None of the fish studied were found to be in this developmental stage. However, a few transparent ripe eggs were found in an individual classified as Stage III. The largest of these eggs was 1.16 mm in diameter with an oil droplet 0.30 mm in diameter. This egg corresponds to Stage V of Rodríguez-Roda (1967). A fish would be classified as being ripe only when a substantial number of eggs of this size are present.

V. Spent—Ovaries are flaccid; completely spent fish had a few degenerating eggs up to 0.63 mm in diameter. Fish in this stage taken in the summer and early fall months had ovaries with a large amount of fatty tissue. GSI >0.2 but <2.0.

Size and reproductive data by estimated age and month are presented in Table 2 for 81 small and medium female bluefin tuna from the Middle Atlantic Bight of the western Atlantic and for 15 small and medium eastern Atlantic female bluefin tuna collected by Rodríguez-Roda (1967) and by Cort et al. (1976). Relatively

TABLE 2.—Length, weight, and gonadal data for 81 small and medium female western Atlantic bluefin tuna collected during 1974-77 and for 15 small and medium female eastern Atlantic bluefin collected during 1963 by Rodríguez-Roda (1967) and during 1976 by Cort et al. (1976).

		Fork length (cm)			Round weight (kg)			Ovary weight (g)			Gonosomatic index (%)			
Age	Month	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	Number
							Western Atlantic							
3	June	100	0.59	97-102	19.6	0.57	16.3-23.2	25	3.9	5-52	0.1	0.02	0.03-0.28	12
	July	98		95-100	18.7		16.8-21.8	16		10-23	0.1		0.06-0.14	6
	August	101		98-105	20.7		18.8-22.2	18		8-51	0.1		0.03-0.23	6
4	June	108		107-109	25.4		24.5-26.3	15		10-20	0.1		0.04-0.08	2
	July	121		118-122	34.2		26.8-38.1	76		68-80	0.2		0.21-0.26	3
	August	115		106-124	29.5		19.1-40.9	49		17-94	0.2		0.09-0.26	4
5	June	133	1.42	126-138	44.1	1.18	36.3-49.9	97	9.5	44-148	0.2		0.11-0.33	12
	July	133		126-140	47.2		43.6-50.8	190		149-231	0.4		0.29-0.53	2
	August	129		126-131	41.0		37.9-45.4	69		40-119	0.2		0.11-0.26	4
6	June	150	1.44	142-157	59.1	2.34	45.4-75.4	204	18.5	102-222	0.4	0.03	0.17-0.51	12
	August	150			58.1			126			0.2			1
7	June	163	0.90	157-169	80.2	2.53	65.4-91.7	434	97.9	175-1,605	0.5	0.10	0.17-1.75	14
	July	160		158-165	60.3		53.1-68.1	142		62-211	0.2		0.13-0.31	3
							Eastern Atlantic							
4	July	111			[1]26.2			150			0.6			1
5	May	130			54.0			740			1.4			1
	June	125			[1]37.0			500			1.4			1
	July	126			[1]37.8			450			1.2			1
	August	134			48.0			460			1.0			1
6	June	149			[1]61.7			900			1.5			1
	July	148			[1]61.0			860			1.4			3
	August	152			63.5			470			0.7			2
7	June	171			110.0			1,920			1.9			1
8	May	180			113.0			2,500			2.2			1
	August	185			106.0			660			0.6			2

[1]Round weight estimated using functional regression of Baglin (1980).

little development towards maturity was evident in the age 1 through age 7 western Atlantic fish with the exception of one age 7 fish collected in June with a GSI of 1.75. The eastern Atlantic small and medium fish, on the average, have a larger mean GSI than the western Atlantic small and medium fish. The largest GSI (2.2) calculated from the eastern Atlantic small- and medium-sized bluefin tuna was found for a fish captured during May at an estimated age of 8 yr.

Body and ovary size, by month, for 403 western and 75 eastern Atlantic female giant bluefin tuna are presented in Table 3, with the calculated monthly GSI presented in Figures 1 and 2. The average body and ovary size of the female giant fish from the western Atlantic was larger than that of the eastern Atlantic fish for each month. Well-developed ovaries were present in western Atlantic giant bluefin tuna during April and May. These fish were collected from the Gulf of Mexico longline and sport fishery and from the Florida Straits sport fishery. Ovarian development was minimal during October, as indicated by a low mean GSI,

TABLE 3.—Length, weight, and gonadal data for 403 female giant western Atlantic bluefin tuna collected during 1965-68, 1974-78, and for 75 female giant eastern Atlantic bluefin tuna collected during 1963 by Rodríguez-Roda (1967).

Month	Fork length (cm)			Round weight (kg)			Ovary weight (g)			Number
	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	
Western Atlantic										
March	237	3.5	199-256	245	10.2	143-307	2,849	448	331-6,810	25
April	242	2.7	190-264	262	8.1	117-335	8,380	564	409-13,166	41
May	240	1.4	205-269	244	4.8	156-324	7,708	475	900-14,960	73
June	246	1.7	213-270	262	5.8	159-351	5,023	341	950-13,600	68
July	254	1.0	218-272	295	3.3	205-375	1,927	89	600-7,000	96
August	257	1.3	224-282	320	4.4	213-424	2,857	158	600-6,250	79
Sept.	256	3.1	235-269	330	7.5	297-374	2,770	533	750-6,500	11
Oct.	242	3.8	212-257	308	16.8	186-370	1,137	71	700-1,400	10
Eastern Atlantic										
May	211	1.8	200-225	190	4.2	155-219	2,758	318	1,540-6,820	17
June	213	2.6	204-230	189	5.9	167-235	3,148	403	1,780-6,280	12
July	214	2.3	189-244	169	5.8	130-263	1,493	117	700-3,580	30
August	207	2.2	197-232	149	5.6	125-226	1,112	85	840-1,980	16

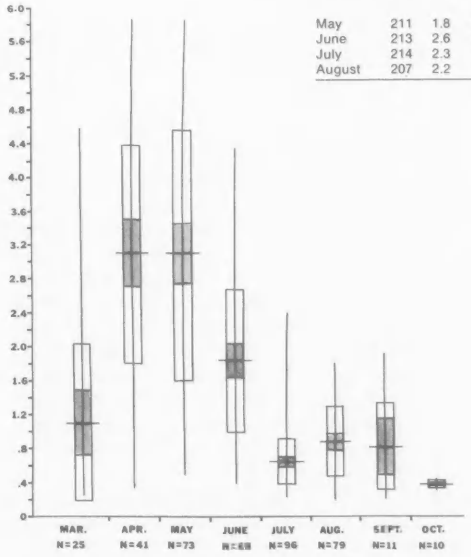


FIGURE 1.—Seasonal variation in gonosomatic index of 403 female giant western Atlantic bluefin tuna collected from 1965 through 1968 and 1974 through 1978. The number, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each side of the mean (shaded box) are shown.

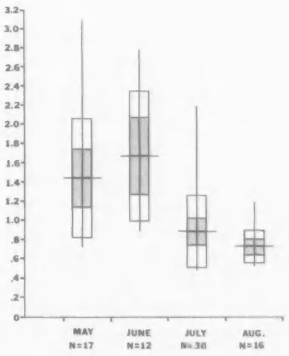


FIGURE 2.—Seasonal variation in gonosomatic index of 75 female giant eastern Atlantic bluefin tuna collected during 1963 by Rodríguez-Roda (1967). The number, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each of the mean (shaded box) are shown.

and reached a peak during April and May as indicated by the highest GSI. Sampling was inadequate for November through February. Well-developed ovaries were present mainly during May and June in eastern Atlantic giant bluefin tuna from the traps at Barbate (Rodríguez-Roda 1967). In May, the mean GSI for the western Atlantic was greater than that for the eastern Atlantic. No great difference was found between the mean GSI for the western and eastern Atlantic giant bluefin tuna for June, July, and August for which data were available for comparison. The plots of the GSI indicate that giant bluefin tuna spawning occurs earlier in the western Atlantic (the drop in GSI occurring in June) than in the eastern Atlantic (the drop in GSI occurring in July).

Heterogeneity of Egg Diameters

A significant difference in egg diameters was found for the center, midregion, and periphery of the anterior section of an ovary from a mature fish ($F = 6.1$; df = 2, 631; $P < 0.005$). No significant difference in egg diameters was found for the center, midregion, and periphery of the middle or posterior sections of the ovary. A significant difference in egg diameters was also found among the anterior, middle, and posterior sections ($F = 11.6$; df = 2, 1,843; $P < 0.001$). Because some heterogeneity occurred, estimates of fecundity were based on eggs from each section of both ovaries. Heterogeneity of egg size within an ovary has also been shown for albacore, *Thunnus alalunga*, (Otsu and Uchida 1959); swordfish, *Xiphias gladius*, (Uchiyama and Shomura 1974); and white marlin, *Tetrapturus albidus*, (Baglin 1979).

Histology of the Ovaries

Microscopic examinations were made of ovarian tissues from 119 small and medium bluefin tuna and 173 giant bluefin tuna. Diameters measured from these prepared slides were considerably smaller than those measured from whole eggs fixed in 10% Formalin (see footnote 5).

The oocytes were grouped into the following stages of oogenesis using the system of Kraft and Peters (1963), Smith (1965), and Moe (1969).

Stage 1—Thin layer of cytoplasm surrounding a relatively large nucleus with a single nucleolus; oocytes are <0.03 mm in diameter.

Stage 2—Dark cytoplasm and many peripheral nucleoli are in the nucleus oocytes are 0.03 mm through 0.13 mm in diameter (resting stage).

Stage 3—Yolk vesicles appear in cytoplasm; the membrane called the zona radiata, also referred to as zona pellucida (Hoar 1969) and vitelline membrane (Bodola 1966), appears at the end of this stage; oocytes are 0.17 mm through 0.30 mm in diameter (early vitellogenic stage).

Stage 4—Thick zona radiata, yolk vesicles, and yolk globules are present; oocytes are 0.33 mm through 0.63 mm in diameter (late vitellogenic stage).

Stage 5—This final stage was seldom observed during histological analysis. It evidently takes place during a short period of time immediately before ovulation. Eggs in this stage have a lightly staining granular yolk mass with few yolk vesicles and yolk globules, a thin zona radiata, and an irregular shape caused by sectioning.

Histological examination of female bluefin ovary sections from the Middle Atlantic Bight revealed the following:

Age 1—Very little sexual differentiation was present in age 1 bluefin tuna ($N = 17$) collected during May, June, July, and August. Some oogonia were observed within the lamellae.

Age 2—The first appearance of oocyte development occurred in age 2 bluefin tuna collected during July ($N = 4$). Both stage 1 and stage 2 oocytes were present, although stage 2 oocytes were most numerous.

Age 3—Many stage 2 oocytes and a few stage 1 oocytes were found in age 3 bluefin tuna collected during January and June ($N = 13$). Only stage 2 oocytes were found in age 3 bluefin tuna collected during July and August ($N = 10$).

Age 4—Stage 2 oocytes were present in all age 4 females collected during June ($N = 36$) (Fig. 3). Also in 11% of these fish, some vitellogenic stage 3 oocytes undergoing absorption were present. Only stage 2 oocytes were present in age 4 bluefin tuna collected during July and August ($N = 10$).

Age 5—Mostly stage 2 oocytes were present in age 5 fish collected during June ($N = 16$),

FIGURE 3.—Ovarian tissue from an age 4 bluefin tuna (119 cm, 33.6 kg) collected off the Middle Atlantic Bight during June 1977. Stage 2 oocytes are present, as indicated by arrow.

although a few stage 1 oocytes were also observed. Also, in 44% of these fish some stage 3 oocytes were present, many undergoing absorption. One individual also had some stage 4 oocytes present. These oocytes were in the process of degeneration. Mostly stage 2 oocytes were present in age 5 fish collected during July ($N = 2$). Both of these fish also had some stage 3 oocytes present, which were undergoing absorption. Stage 2 oocytes were present in all fish collected during August ($N = 4$). Only one of these fish had stage 3 oocytes present. These stage 3 oocytes were also undergoing absorption.

Age 6—The majority of oocytes observed in age 6 bluefin tuna collected during June ($N = 12$) were in stage 2 of development and only a few stage 1 oocytes were observed. Many of these fish (83%) had some stage 3 oocytes present, most undergoing the process of degeneration (Fig. 4). One individual had some stage 4 oocytes present, which were also degenerating. Only stage 2 oocytes were found in an age 6 bluefin tuna collected during August.

Age 7—Mostly stage 2 oocytes were found in age 7 fish collected during June ($N = 15$). Also, some stage 1 oocytes were present in most of these fish and 47% had stage 3 oocytes present, many of which were undergoing absorption. Only stage 2 oocytes were found in an age 7 fish collected during July and another age 7 fish taken during October.

Some gonadal development, therefore, occurs in these medium female bluefin tuna. However, the simulation of gonadal maturation by young fish that probably do not spawn has been reported for king mackerel, *Scomberomorus cavalle*, (Beaumariage 1973) and Atlantic sailfish, *Istiophorus platypterus*, (Jolley 1977). These authors based their determination on the size of the stage 4 oocytes, on their compactness within the lamellae, and on the appearance of many degenerating oocytes. My observations of medium bluefin tuna seem to correspond with the findings of the above authors, although the most

FIGURE 4.—Ovarian tissue from an age 6 bluefin tuna (153 cm, 59.5 kg) collected off the Middle Atlantic Bight during June 1976. Resting stage 2 oocytes are present (upper arrow), as are stage 3 oocytes undergoing the process of degeneration (lower arrow).

developed oocytes in the majority of fish that I examined were in stage 3 of development, and the average were in stage 2 based on the mean size of the oocytes measured (Fig. 5).

I believe, therefore, that the Middle Atlantic Bight is not a significant spawning area during the summer and probably not at any other time of the year, but samples are not available for other seasons. Also, recently there has been speculation by Rivas (1978) that some of these medium bluefin tuna may migrate during May and June across the Atlantic to the Mediterranean Sea to spawn. According to Sella (1929) eastern Atlantic bluefin tuna begin to reproduce in their third year, when they attain a weight of about 15 kg. Rodríguez-Roda (1967) found that 50% of eastern Atlantic bluefin tuna females are mature at 97.5 cm or 3 yr of age. However, the smallest bluefin tuna that he estimated fecundity for was 130.5 cm and 54 kg, which corresponds to an age 5 fish according to Coan (1976). Frade and Manaças (1933) found very little development in age 3 females from the eastern Atlantic. Cort et al. (1976) found developing oocytes in eastern Atlantic bluefin tuna measuring 148 and 152 cm from the Gulf of Gascony. These fish would be age 6 according to Coan (1976).

The only published record I have found of age of maturity of western Atlantic bluefin tuna is that of Westman and Neville (1942). Observing the gross morphology of ovaries, they indicated that western Atlantic bluefin tuna 5 yr of age appeared to be mature, although the gonads gave no indication of the presence of eggs. I have also examined the unpublished cruise report of the MV *Delaware*, June 1957. Using the conversion table of Coan (1976), all age 3 female bluefin tuna were judged immature, and most age 4 (2 out of 3) were judged immature. No description of the ovaries on an age 5 fish was given, and 67% of age 6 females ($N = 6$) had well-developed eggs.

My analysis of western Atlantic bluefin tuna ovaries indicates that age 6 would probably be

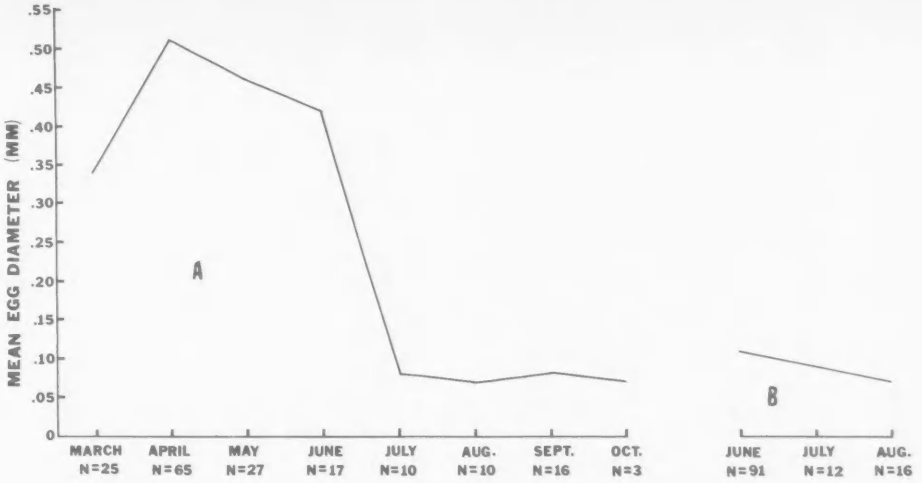


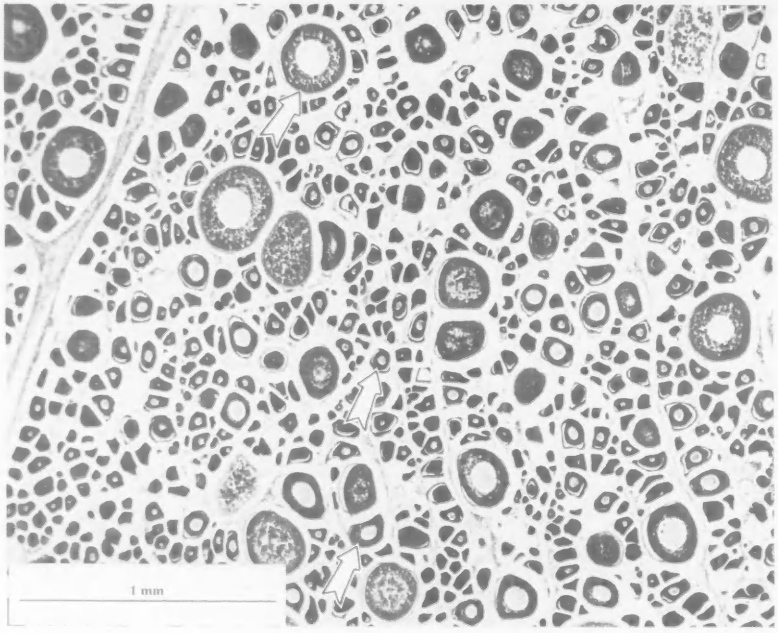
FIGURE 5.—Mean egg diameter of largest ovarian egg as determined from histological sections from monthly samples (N) of A) female giant bluefin tuna from the Gulf of Mexico and the Florida Straits (March through June 1955, 65-67, 76-78) and from off New England (July through October 1974-75, 77), and B) female bluefin tuna ages 3-7 from off the Middle Atlantic Bight (June through August 1974-77).

the earliest age at which a majority of females could possibly reach maturity. However, a majority of vitellogenic oocytes in these age 6 fish were being absorbed and most likely would not have been spawned during the years when these fish were taken. As previously noted, I observed no vitellogenic oocytes in age 3 fish, but if Sella (1929) and Rodríguez-Roda (1967) are correct, eastern Atlantic bluefin tuna may reach maturity at an earlier age than their western Atlantic counterparts.

Vitellogenic oocytes were not found in the two giant bluefin tuna (205 and 207 cm) taken during the March 1966 MV *Delaware* Cruise 66-2 (lat. 37°24′N, long. 67°32′W). Vitellogenic oocytes were found in one of three giant fish (190-213 cm) taken during April 1965 on the MV *Delaware* Cruise 65-3 (lat. 35°54′N, long. 72°51′W). Evidently this area of the western North Atlantic was not an important spawning area for bluefin tuna during March-April.

Vitellogenic oocytes (stages 3 or 4) were present in all giant bluefin tuna taken from the Gulf of Mexico and Florida Straits during 1955, 1967, 1976, 1977, and 1978 during March (N = 24), April (N = 61), and May (N = 54) (Figs. 6, 7). In one of two fish taken in June 1967 and 1977, stage 3 and stage 4 oocytes were present; in the other fish all the vitellogenic oocytes had been spawned or absorbed. On the average, the largest oocytes in all of the fish for July (N = 10), August (N = 10), September (N = 16), and October (N = 12) from off New England during 1974, 1975, and 1977 were in stage 2 (Fig. 8). Vitellogenic oocytes were generally absent from these fish.

I found degeneration and absorption of advanced unovulated eggs more common as the season progressed. This agrees with the findings of Frade and Manaças (1933) for eastern Atlantic bluefin tuna. Distinctive atretic bodies, formed from the remnants of oocytes that were not shed, were present in the female giant bluefin tuna collected during March through October. Topp and Hoff (1971) also reported atretic body formation in the ovaries of a single giant female collected from the west Florida coast during May. As previously described by Smith (1965), these atretic bodies form a characteristic brownish mass, the corpus atreticum, and are made up of amorphous brownish granules, phagocytes, and clear yellow pigment globules (Fig. 9). I found that empty follicles left behind after the ripe oocytes are released degenerate rapidly. This was also observed for eastern Atlantic bluefin tuna by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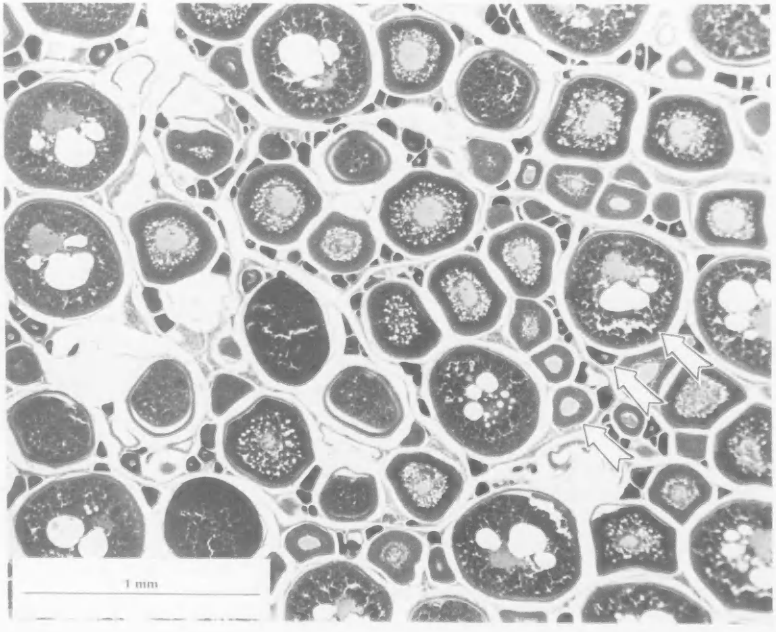
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FIGURE 6.—Ovarian tissue from a giant bluefin tuna (250 cm) collected off the Gulf of Mexico during March 1978. Early stage 4 oocytes (upper arrow), stage 2 oocytes (middle arrow), and stage 3 oocytes (lower arrow) are present.

FIGURE 7.—Ovarian tissue from a giant bluefin tuna (205 cm) collected off the Gulf of Mexico during May 1978. Late stage 4 oocytes (upper arrow), stage 2 oocytes (middle arrow), and stage 3 oocytes (lower arrow) are present.

Frade and Manaças (1933), who speculated that the rapid degeneration of the follicles could be caused by pressure exerted by neighboring oocytes. My findings also confirm that western Atlantic bluefin tuna released eggs intermittently during April, May, and June, the majority during May.

Fecundity Estimates

Fecundity estimates were obtained for 28 western Atlantic bluefin tuna, which were collected from the Gulf of Mexico and Florida Straits during April, May, and June of 1967, 1968, 1974, 1975, 1976, and 1978 (Table 4). The reliability of the dry gravimetric method was tested by estimating the fecundity of an individual fish by counting and weighing eggs from four subsamples. Based on these four estimates, the average number of eggs >0.46 mm in diameter was 41.6 million with a range from 40.0 to 43.0 million and a standard error of the mean (SE) of 0.76. The average number of eggs >0.32 mm in diameter was 76.0 million with a range from 72.5 to 82.5 million and SE = 2.2.

I am presenting two estimates of potential fecundity, and the estimate based on eggs >0.32 mm in diameter essentially coincides with the size of 0.33 mm used by Rodríguez-Roda (1967) for eastern Atlantic bluefin tuna. This would be the potential number of eggs that could be spawned, assuming there was no degeneration or absorption of advanced unovulated eggs. My histological examinations of bluefin ovaries,

FIGURE 8.—Ovarian tissue from a giant bluefin tuna (256 cm, 268 kg) collected off the northeast coast of the United States during August 1975. Stage 2 oocytes are present, as indicated by arrow.

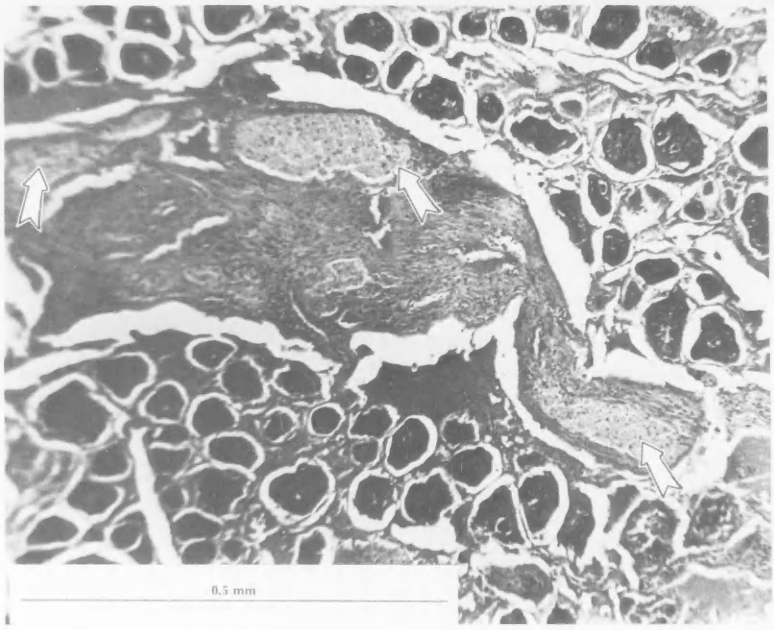

FIGURE 9.—Ovarian tissue from a giant bluefin tuna (264 cm, 297 kg) collected off the northeast coast of the United States during July 1975. Brown bodies are present, as indicated by arrows.

however, revealed the presence of atretic bodies. It was impossible to quantify the number of eggs constituting these atretic bodies, although I assume that absorption would occur principally with the smaller vitellogenic ova. Therefore, I have also estimated the number of eggs >0.46 mm in the most advanced size mode that could potentially be spawned during one spawning season. For bluefin tuna 205-269 cm FL and 156-324 kg round weight, the average number of eggs 0.33 mm in diameter and larger was estimated as 60.3 million (SE = 4.04) and the average number of eggs 0.47 mm in diameter and larger was estimated as 34.2 million (SE = 2.15). No apparent relationship was found for fecundity as a function of length or estimated weight for the size range of bluefin tuna I studied. MacGregor (1968) said that the relationships of length and weight to egg production are masked in many species of fish, because egg production occurs over a relatively short range in size, and because variation in number of eggs produced at each length is great. Bailey (1964) found no obvious relationship between fecundity and fish size for American smelt, *Osmerus mordax*. Schenck and Whiteside (1977) and Loesch and Lund (1977) found a great amount of variability in fecundity for a given fish size for the fountain darter, *Etheostoma fonticola*, and blueback herring, *Alosa aestivalis*. Since histological examinations of ovaries and estimated GSI showed that the bluefin tuna are multiple spawners, it is possible that some of the fish selected for fecundity estimates had previously shed eggs. Also the rate of absorption of vitellogenic ova could have varied for the fish selected for fecundity estimates. I found, however, that the dry weight of eggs could be used for estimating fecundity. The following relationships were found:

$$F = 5.2895 + 0.0167\ W\ (R^2 = 0.64),$$

where F is the number of ova >0.46 mm in diameter and W is the dry weight of all eggs separated from the ovarian connective tissue.

TABLE 4.—Length, weight, and gonadal data for 28 female western Atlantic bluefin tuna from the Gulf of Mexico and the Florida Straits collected during April, May, and June 1967, 1968, 1974, 1975, 1976, and 1978. The mean and standard error of the mean are given at the bottom of the columns.

Body length (cm)	Estimated body weight (kg)	Dry weight of eggs (g)	Gonosomatic index (%)	Estimated no. of eggs >0.46 mm diameter (millions)	Estimated no. of eggs >0.32 mm diameter (millions)
205	156	1,260	5.3	13.6	32.7
222	[1]188	696	2.1	16.7	22.7
229	217	1,202	3.1	24.2	46.4
229	217	2,177	5.0	55.5	96.0
229	217	1,481	2.8	33.9	64.4
231	224	1,330	4.4	26.8	41.1
236	[1]197	1,329	3.2	28.4	40.3
236	[1]189	1,404	3.2	29.6	44.7
238	246	1,788	4.1	39.0	63.9
238	246	1,703	4.2	40.1	64.5
238	246	1,796	3.8	34.4	61.7
241	254	1,483	3.4	29.8	62.4
241	254	2,436	4.8	48.0	84.9
241	[1]247	1,560	3.9	33.0	44.0
244	263	1,750	3.6	25.2	56.7
244	263	1,452	3.4	23.2	42.1
244	263	2,121	5.0	49.3	93.3
252	289	2,770	4.7	39.6	94.6
254	298	1,942	2.9	41.6	76.0
—	307	1,681	2.5	32.0	59.2
256	307	1,950	2.6	42.2	79.5
257	[1]232	1,200	2.9	24.3	33.8
257	309	750	1.9	16.2	26.2
259	316	2,750	4.2	32.6	76.9
259	316	2,500	4.4	48.8	80.6
261	[1]272	1,488	2.6	31.4	42.3
262	[1]324	2,593	4.5	57.6	81.6
269	[1]284	1,950	4.6	40.6	74.8
$\bar{X}$ 243	255	1,734	3.7	34.2	60.3
SE 2.78	8.37	102.79	0.18	2.15	4.04

[1]Actual weight determined.

$$F = -0.9057 + 0.0353\ W\ (R^2 = 0.81),$$

where F is the number of ova >0.32 mm in diameter and W is the dry weight of all eggs separated from the ovarian connective tissue.

A reduction in fecundity in older fish has been reported by Bodola (1966) for gizzard shad, *Dorosoma cepedianum*, and by Loesch and Lund (1977) for blueback herring. No such decline in number of eggs was found for western Atlantic bluefin tuna.

My fecundity estimates for western Atlantic bluefin tuna are considerably greater than the estimate given by Williamson (1962). He, however, did not describe how he arrived at his estimate for a western Atlantic bluefin tuna. My estimates more closely agree with estimates presented by Frade (1950) and Rodríguez-Roda (1967) for eastern Atlantic bluefin tuna. Although my estimates were based generally on larger fish, it appears that western Atlantic bluefin tuna are considerably more fecund than eastern Atlantic bluefin tuna.

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LITERATURE CITED

BAGLIN, R. E., JR.
1976. A preliminary study of the gonadal development and fecundity of the western Atlantic bluefin tuna. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 5 (SCRS-1975):279-289.
1979. Sex composition, length-weight relationship, and reproduction of the white marlin, *Tetrapturus albidus*, in the western North Atlantic Ocean. Fish. Bull., U.S. 76:919-926.
1980. Length-weight relationships of western Atlantic bluefin tuna, *Thunnus thynnus*. Fish. Bull., U.S. 77:995-1,000.

BAGLIN, R. E., JR., AND L. R. RIVAS.
1977. Population fecundity of western and eastern North Atlantic bluefin tuna, *Thunnus thynnus*. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 6 (SCRS-1976):361-365.

BAILEY, M. M.
1964. Age, growth, maturity, and sex composition of the American smelt, *Osmerus mordax* (Mitchill), of Western Lake Superior. Trans. Am. Fish. Soc. 93:382-395.

BEAUMARIAGE, D. S.
1973. Age, growth, and reproduction of king mackerel, *Scomberomorus cavalla*, in Florida. Fla. Mar. Res. Publ. 1, 45 p.

BERRIEN, P. L., M. P. FAHAY, A. W. KENDALL, JR., AND W. G. SMITH.
1978. Ichthyoplankton from the RV DOLPHIN survey of Continental Shelf waters between Martha's Vineyard, Massachusetts and Cape Lookout, North Carolina 1965-66. Sandy Hook Lab. Northeast Fish. Cent., Natl. Mar. Fish. Serv. Tech. Ser. Rep. 15, 152 p.

BODOLA, A.
1966. Life history of the gizzard shad, *Dorosoma cepedianum* (Lesueur), in Western Lake Erie. U.S. Fish Wildl. Serv., Fish. Bull. 65:391-425.

BUÑAG, D. M.
1956. Spawning habits of some Philippine tuna based on diameter measurements of the ovarian ova. Philippine J. Fish. 4:145-175.

COAN, A.
1976. Length, weight, and age conversion tables for Atlantic tunas. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 5 (SCRS-1975):64-66.

CORT, J. L., C. A. FERNANDEZ PATO, AND E. DE CARDENAS.
1976. Observations sur la maturation sexuelle du thon rouge, *Thunnus thynnus* (L.), du golfe de Gascogne. Cons. Int. Explor. Mer, 6 p.

ERDMAN, D. S.
1968. Spawning cycle, sex ratio, and weights of blue

marlin off Puerto Rico and the Virgin Islands. Trans. Am. Fish. Soc. 97:131-137.

FRADE, F.
1950. Estudos de pescarias do ultramar Portugues os atuns. Minist. Colón. Junta Invest. Colon., Lisbon, 30 p.

FRADE, F., AND S. MANACAS.
1933. Sur l'état de maturité des gonades chez le thon rouge génétique (note Préliminaire). C. R. Assoc. Anat., 15 p.

GIBBS, R. H., JR., AND B. B. COLLETTE.
1967. Comparative anatomy and systematics of the tunas, genus *Thunnus*. U.S. Fish Wildl. Serv., Fish. Bull. 66:65-130.

HOAR, W. S.
1969. Reproduction. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. III, p. 1-72. Acad. Press, N.Y.

JOLLEY, J. W., JR.
1977. The biology and fishery of Atlantic sailfish, *Istiophorus platypterus*, from southeast Florida. Fla. Mar. Res. Publ. 28, 31 p.

KRAFT, A. N., AND H. M. PETERS.
1963. Vergleichende Studien über die Oogenese in der Guttung Tilapia (Cichlidae, Teleostei). Z. Zellforsch. Mikrost. Anat. 61:434-485.

LOESCH, J. G., AND W. A. LUND, JR.
1977. A contribution to the life history of the blueback herring, *Alosa aestivalis*. Trans. Am. Fish. Soc. 106:583-589.

MACGREGOR, J. S.
1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. Calif. Dep. Fish Game 54:281-288.

MATHUR, D., AND J. S. RAMSEY.
1974. Reproductive biology of the rough shiner, *Notopis baileyi*, in Halawakee Creek, Alabama. Trans. Am. Fish. Soc. 103:88-93.

MOE, M. A., JR.
1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes), from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour. Mar. Res. Lab., Prof. Pap. Ser. 10, 91 p.

MONTOLIO, M., AND M. JUAREZ.
1977. El desove de *Thunnus thynnus thynnus* en el Golfo de Mexico - Estimado preliminar de la magnitud de la poblacion en desove a partir de la abundancia de larvas. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 6 (SCRS-1976):337-344.

OTSU, T., AND R. N. UCHIDA.
1959. Sexual maturity and spawning of albacore in the Pacific Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 59:287-305.

PARKS, W. W.
1977. Cohort and equilibrium yield-per-recruit analyses for the Atlantic bluefin tuna fisheries system accounting two system configurations and two natural mortality models. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 6 (SCRS-1976):385-4.

PARRACK, M. L.
1980. Trends on the abundance and age structure of Atlantic bluefin tuna. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 9 (SCRS-1979):563-580.

PETERSON, C. L.
1961. Fecundity of the anchoveta (*Cetengraulis mysticetus*) in the Gulf of Panama. Inter-Am. Trop. Tuna Comm. Bull. 6:55-68.

RICHARDS, W. J.
1976. Spawning of bluefin tuna (*Thunnus thynnus*) in the Atlantic Ocean and adjacent seas. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 5 (SCRS-1975):267-278.

RIVAS, L. R.
1954. A preliminary report on the spawning of the western north Atlantic bluefin tuna (*Thunnus thynnus*) in the Straits of Florida. Bull. Mar. Sci. Gulf Caribb. 4:302-322.
1978. Preliminary models of annual life history cycles of the North Atlantic bluefin tuna. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 369-393. Acad. Press, San Franc.
1979. Proposed terminology for size groups of the North Atlantic bluefin tuna (*Thunnus thynnus*). Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 8 (SCRS-1978):441-446.

RODRÍGUEZ-RODA, J.
1964. Biología del Atún, *Thunnus thynnus* (L.), de la costa sudatlántica de España. Invest. Pesq. 25:33-146.
1967. Fecundidad del atún, *Thunnus thynnus* (L), de la costa sudatlántica de España. Invest. Pesq. 31:33-52.

SCHENCK, J. R., AND B. G. WHITESIDE.
1977. Reproduction, fecundity, sexual dimorphism and sex ratio of *Etheostoma fonticola* (Osteichthyes:Percidae). Am. Midl. Nat. 98:365-375.

SELLA, M.
1929. Migrations and habitat of the tuna (*Thunnus thynnus* L.), studied by the method of the hooks, with observations on growth, on the operation of the fisheries, etc. Translated by W. G. Van Campen, U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 76, 20 p.

SHINGU, C., AND K. HISADA.
1980. Analysis on the Atlantic bluefin tuna stock. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 9 (SCRS-1979):595-600.

SMITH, C. L.
1965. The patterns of sexuality and the classification of serranid fishes. Am. Mus. Novit. 2207, 20 p.

TOPP, R. W., AND F. H. HOFF.
1971. An adult bluefin tuna, *Thunnus thynnus*, from a Florida west coast urban waterway. Fish. Bull., U.S. 69:251-252.

UCHIYAMA, J. H., AND R. S. SHOMURA.
1974. Maturation and fecundity of swordfish, *Xiphias gladius*, from Hawaiian waters. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers, p. 142-148. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

VLADYKOV, V. D.
1956. Fecundity of wild speckled trout *Salvelinus fontinalis* in Quebec lakes. J. Fish. Res. Board Can. 13:799-841.

WESTMAN, J. R., AND W. C. NEVILLE.
1942. The tuna fishery of Long Island, New York. N.Y. Board Superv., Nassau Cty., 30 p.

WILLIAMSON, G. R.
1962. The bluefin tuna in Newfoundland waters. Newfoundland Tourist Dev. Off., Saint John's, Newfoundland, Can., 23 p.

AN EVALUATION OF TECHNIQUES FOR TAGGING SMALL ODONTOCETE CETACEANS

A. B. IRVINE,[1] R. S. WELLS,[2] AND M. D. SCOTT[3]

ABSTRACT

Ninety tags—various combinations of radio tags, spaghetti tags, Roto tags, freeze brands, and tags bolted to the dorsal fin—were placed on 47 Atlantic bottlenose dolphins, *Tursiops truncatus*, captured near Sarasota, Florida, between January 1975 and July 1976. In 18 months of field observation, 910 tagged dolphins were sighted; 781 were identifiable, and 129 were not. Twelve naturally marked dolphins were also observed. Radio tagged animals were tracked for as long as 22 days. Repeated observations of tagged animals permitted evaluation of effect on animals and relative merits of the various tags. Freeze brands were most readable from a distance (≤30 m), and most long lived (4.8 years). Other tags were too short lived (bolt tags) or too small to be identified from a distance (Roto tags and spaghetti tags), and all caused tissue destruction. Radio tags caused unexpected dorsal fin damage and were frequently lost prematurely. Taken together, the results suggest that freeze brands are least harmful, and that static tags should be tested on each species to be studied prior to attachment in the field.

Cetaceans are difficult to study in the field. Most individuals move almost constantly, rise to the surface only briefly to breathe, and are difficult to differentiate from conspecifics. To facilitate individual recognition, researchers have developed several tagging techniques and tested them on small odontocete cetaceans. Nishiwaki et al. (1966) placed streamer tags on captive rough-toothed dolphins, *Steno bredanensis*, and concluded that none were effective. On the other hand Perrin et al. (1979) recovered spaghetti tags, another type of streamer, from free-ranging dolphins, *Stenella* spp., in the eastern tropical Pacific up to 1,478 d after attachment. Roto tags were placed on the spotted dolphin, *S. attenuata*, and one marked individual was repeatedly identified from a semisubmersible over a period of 3½ yr (Norris and Pryor 1970). Evans et al. (1972) successfully used radio transmitters, large plastic "button" tags, spaghetti tags, and freeze brands on a total of five species in the Pacific Ocean and Gulf of Mexico. Leatherwood and Evans (1979) have recently reviewed developments and uses of radio tags on cetaceans. Irvine and Wells (1972) reported that an improved button tag was sighted 3 mo after attachment to a bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Fla. Despite all these improvements in tagging technology, however, little information has been available about long-term effectiveness or affect on the wearers of any type of tag.

The tagging program of Irvine and Wells (1972) was reinitiated in the same area in January 1975, after a 4-yr lapse. Using radio transmitters, visual tags, and natural marks we studied the movements and activities of bottlenose dolphins. Between 29 January 1975 and 25 July 1976, 47 dolphins were captured, tagged, and released a total of 90 times. A summary of the tagging program and an evaluation of the tagging methods used are included below. Detailed analysis of the tagging program results is presented by Irvine et al. (1979,[4] 1981).

METHODS

The study was conducted along 40 km of coast south from Tampa Bay, Fla. The study area included shallow channels and bays bounded by a chain of barrier islands (NOS Chart No.

[1]Gainesville Field Station, Denver Wildlife Research Center, 412 NE. 16th Ave., Gainesville, FL 32601.

[2]Department of Zoology, University of Florida, Gainesville, Fla.; present address: Center for Coastal Marine Studies, University of California, Santa Cruz, Santa Cruz, CA 95064.

[3]Department of Zoology, University of Florida, Gainesville, Fla.; present address: Inter-American Tropical Tuna Commission, Scripps Institute of Oceanography, La Jolla, CA 92037.

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[4]Irvine, A. B., M.D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. A study of the movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-298042, 54 p.

11425). Dolphins were captured by encircling one to nine animals with a 455 m × 4.5 m net dropped from a fast moving boat in shallow water. An inner circle enclosure method (Asper 1975) was used to minimize escapes. The inner circle was partitioned so that individual dolphins could be isolated and entangled without collapsing the entire net on remaining animals. Tangled dolphins were removed from the net and placed for tagging in a stretcher, usually held in the water alongside a boat. All animals were sexed, measured, and photographed before tagging. Previously tagged dolphins were examined and retagged as necessary before being released.

The study area was surveyed as thoroughly as possible at least biweekly in a 7.3 m Wellcraft Fisherman[5] boat equipped with a 3 m tuna tower. All dolphin sightings were recorded during 228 surveys; photographs were taken to facilitate identification of tags and distinctive dorsal fins.

Radio Tags

An improvement (Model PT 219) of the radio tag developed for small pelagic cetaceans by Ocean Applied Research Corporation (Martin et al. 1971) had not been tested on *T. truncatus*. In our first efforts, the transmitter was attached with plastic straps to a foam-lined fiber glass saddle and secured to the dorsal fin with a stainless steel bolt through the fin. Because saddles provided by the manufacturer were too small for most *T. truncatus*, the transmitters were attached to fiber glass saddles molded by the authors (Fig. 1A, C). The saddles were lined with open cell foam to protect the animal from abrasion and to allow water circulation for thermoregulation.

Transmitter saddles were attached using techniques developed by other investigators (see review by Leatherwood and Evans 1979). The first seven saddles were attached with single bolts through the dorsal fin. The last three saddles were attached with bolts fore and aft to provide greater stability against water flow (Fig. 1C). Spring-loaded bolts with dissolving nuts were designed to release the saddle and transmitter from the dolphin sometime after the 1-2 mo life of the lithium batteries.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA, or the U.S. Fish and Wildlife Service.

Ten radio tags (designated RT-1 through RT-10) were attached to dolphins between 29 January 1975 and 9 June 1976. The RT-1 transmitter consisted of a single 35 cm long × 3.7 cm diameter tube with a 63 cm high spring steel antenna on the forward end. Transmissions from RT-1 gradually failed within 2 h, apparently due to saltwater leakage into the battery case. Cause of failure could not be confirmed because the transmitter was missing from the saddle when it was sighted 2 d after attachment. Transmitters on subsequent radio tags were attached to the saddle with bolted aluminum plates (Fig. 1A, C) instead of plastic straps.

The transmitter antenna on RT-2 was observed to be broken off at the base 5 d after attachment. Consequently, transmitter packages on RT-3 through RT-10 were modified to two tubes, 19.2 cm long × 3.8 cm diameter, connected by copper tubing at the forward end. A flexible 42.5 cm high whip antenna extended vertically from the rear of the starboard tube. The tubes, with transmitter assembly in one and batteries in the other, were bolted to either side of the saddle, and the connecting tubing was solidly encased in fiber glass (Fig. 1C).

Visual Tags

The button tags described by Evans et al. (1972) had proven not to be durable on *T. truncatus* (Irvine and Wells 1972). Therefore, we elected to try rectangular fiber glass "visual tags" (Fig. 2). These tags were 10 cm × 7.5 cm and made of 0.4 cm thick yellow laminated fiber glass with 5.1 cm high black tape numerals epoxied to the surface. Each tag was held in place by Teflon bolts with stainless steel washers and cotter pins. The bolts were placed near the anterior edge of the tag to produce a streaming effect as the dolphin moved through the water. The bolt hole was bored through the fin and cauterized with a heated rod, and sheathed with Plexiglas tubing in the same manner as for radio tags.

Double bolt tags, also yellow rectangles with black numerals, were cut from 0.2 cm thick fiber glass and varied in size from 9.0 cm × 12.9 cm to 10 cm × 15 cm, depending on the size of the dorsal fin to be tagged. The bolts were located near the anterior and posterior edges of the tag. Numerals were 7.7 cm high. Because cotter pins had sheared some of the Teflon bolts on single

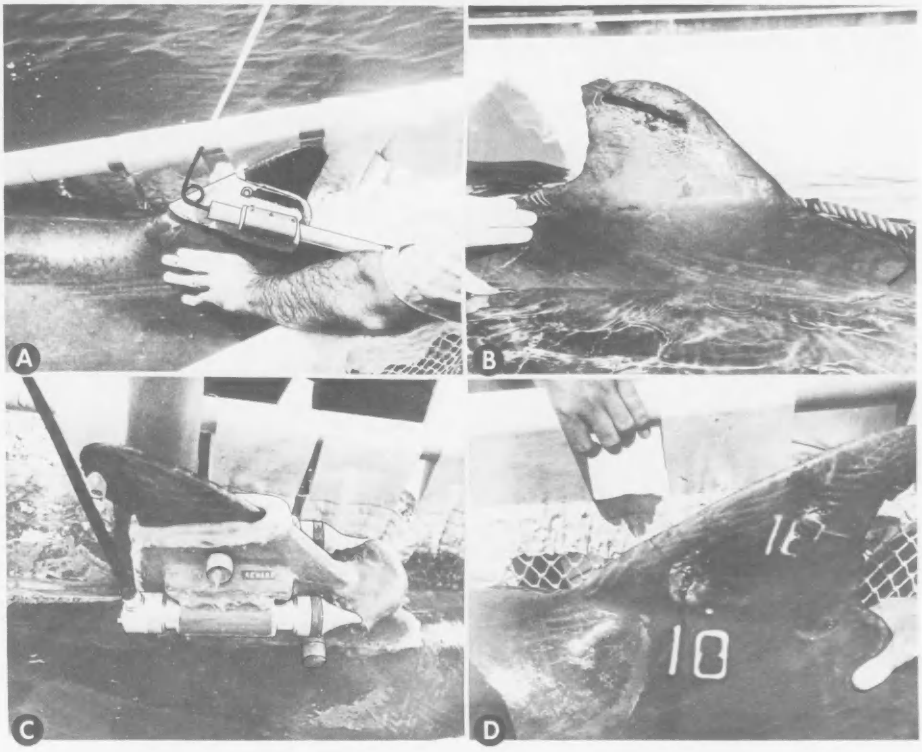

FIGURE 1.—A. Single tube transmitter with spring antenna forward (on dolphin RT-2). B. Dorsal fin 8 mo after transmitter in A was attached. C. Twin tube transmitter assembly with whip antenna aft. Dissolving nuts are top center and below the forward portion of the tube. D. Dorsal fin from C 22 d after the transmitter's installation. Note discolored, apparently necrotic, area around forward hole and apparent migration path of top bolt.

bolt tags, double bolt tags were attached with 0.64 cm stainless steel bolts and nuts.

Freeze Brands

When first captured, all dolphins were freeze branded with 5 cm high numerals on both sides of the dorsal fin and on the body below the fin (Figs. 1D, 2C, D). Recaptured animals were rebranded as necessary to improve visibility of existing brands. Application times of 15 s with irons cooled in a mixture of Dry Ice and alcohol were used to brand the dolphins captured before August 1975. Thereafter, liquid nitrogen was used as the coolant. The application time remained 15 s. When possible, the skin was rubbed with an alcohol swab to lower the skin temperature by evaporative cooling prior to branding. Before April 1976, the branding irons were applied to the skin with a gentle rocking motion to assure even contact. After that time the irons were held firmly against the skin without motion, and brand visibility was greatly improved. In some cases, however, parts of the brand did not show because of uneven contact (Figs. 1D, 2C, D).

Roto Tags

Numbered Roto tags (NASCO Inc., Ft. Atkinson, Wis., Jumbo size) were attached to the trailing edge of the dorsal fin of all dolphins handled after January 1976. Red tags were attached to females and yellow tags to males. The

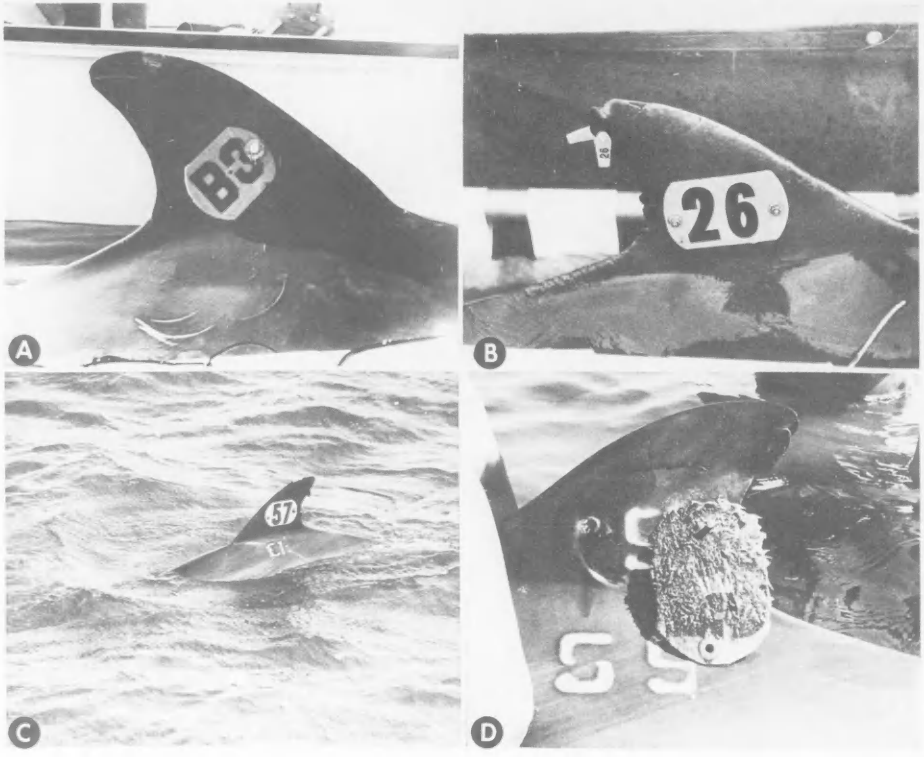

FIGURE 2.—A. Single bolt visual tag held by Teflon bolt and cotter pin. Note tag bolt scar from 1970-71 study. B. Double bolt tag, Roto tag (at top rear of fin), and spaghetti tag (lower right). C. Double bolt tag on free-swimming dolphin. Note freeze brand with incomplete left digit on body below fin. D. Algae-covered tag 2 mo after initial installation. Note indented area of skin where water flow against tag on opposite side of fin caused pressure on near side. Note also discolored tissue around forward bolt hole.

TABLE 1.—Comparison of tagging techniques.

Tag no.	No. tags installed	Tag longevity[1]	No. sightings/tag mean	No. sightings/tag total	No. identifications/tag mean	No. identifications/tag total	% identifiable sightings-other observers	No. tags of known fate	Tags of known fate lost, broken, or removed %	Tags of known fate lost, broken, or removed total no.	Tags of known fate obscured by fouling %	Tags of known fate obscured by fouling total no.	Tags of known fate removed because of tissue damage %	Tags of known fate removed because of tissue damage total no.
Visual tags (single bolt)	16	<5 min to >2 mo	4.88	78	2.00	32	6	14	86	12	14	2	14	2
Visual tags (double bolt)	19	<2 wk to >2 mo	10.00	190	9.84	187	16	16	63	10	31	5	25	4
Roto tags	53	<1 d to >5.5 mo	6.45	342	0.53	28	0	48	40	19	10	5	4	2
Spaghetti tags	17	<1 mo to >13 mo	2.53	43	0		0	12	50	6	0		25	3
Freeze brands	[2]47	>4.8 yr	6.57	309	5.89	277	2	39	—	—	—	—	—	—
Natural marks[3]	12	>5 yr	7.25	87	7.25	87	1	12	—	—	—	—	—	—

[1]Length of time tag was attached and identifiable.
[2]Many were redone or "touched up."
[3]Recognizable dorsal fins.

numbers on the tags were too small to be read from the observation boat, but the color codes were useful for recognition of sex, and the positions of a tag often indicated identity.

Spaghetti Tags

Spaghetti tags (Floy Tag and Manufacturing, Inc., Seattle, Wash., Model FH 69A) were tested on some dolphins captured from April through June 1976. The attachment technique was similar to that described by Evans et al. (1972), except that the tags were applied to animals in a stretcher.

Natural Marks

Some dolphins had disfigured or uniquely shaped dorsal fins. A photo catalog of these recognizable untagged animals was compiled as a reference for field identification.

RESULTS

Nine hundred ten tagged dolphins were sighted; 781 were identifiable, and 129 others were not. When field identification was uncertain, photographs of combinations and locations of tags or tag remnants were often examined to verify individual identities. A compilation of tagging and sighting results is presented in Table 1.

Radio Tags

Ten dolphins were radio tagged and tracked for up to 22 d (Table 2). Eight of these were later recaptured and examined. In five instances, the saddle was lost, apparently because the bolt ripped through the fin (for example, see Figure 1B). Fin damage was apparent 3 to 6 wk after tagging by which time saddles no longer fit snugly over the leading edge of the fin. When loosened, the saddles tilted backwards creating an obvious drag; this shifting caused the bolts to migrate dorsoposteriorly. When RT-8 was recaptured after wearing a transmitter for 22 d, the two bolt holes had not healed nor appeared infected. The forward bolt had migrated dorsoposteriorly about 1.5 cm (Fig. 1D), and the saddle was fouled with algal growth and monofilament line. When RT-9 was recaptured after 46 d, the saddle and rear bolt were missing, but the front bolt was still present but bent, with part of the dissolving nut attached. The partially healed wounds appeared discolored and necrotic, but showed no obvious signs of infection. Only RT-6 showed no fin damage from the radio tag, but the tag (with malfunctioning transmitter) was removed <8 h after attachment.

Two dolphins, RT-9 and RT-10, developed aberrant swimming behavior after 10 and 17 d, respectively. Both animals were observed to respire without bringing the dorsal fin to the surface in a typical cetacean rolling motion, although each could move rapidly under water. Evaluation of the problem was impossible because RT-9 evaded recapture attempts during this period, and RT-10 was not sighted during capture operations.

One animal, RT-7, died 17 d after tagging, apparently of causes unrelated to the radio tag. Necropsy results implicated pulmonary damage from parasitism as a cause of death. It could not be determined if the capture-tagging process contributed to the cause of death. Tissue autolysis precluded histopathological examination, and no parasites were found.

TABLE 2.—Radio tagging results.

Tag no.	Tag description	Dolphin sex	Dolphin length (cm)	Date attached	Duration of transmission	Probable reason for cessation of transmission
RT-1	Single cylinder; forward spring antenna	Male	251	29 Jan. 1975	2 h	Water leak (?)
RT-2	Single cylinder; forward spring antenna	Male	210	28 Apr. 1975	5 d	Broken antenna
RT-3	Twin cylinder; aft spring antenna	Male	249	15 Jun. 1975	20 h[1]	Seawater switch failure (?)
RT-4	Twin cylinder; aft flexible antenna	Female	252	1 Aug. 1975	6 d[2]	Unknown
RT-5	Twin cylinder; aft flexible antenna	Female	257	3 Oct. 1975	7 d[3]	Seawater switch failure (?)
RT-6	Twin cylinder; aft flexible antenna	Male	226	15 Dec. 1975	7 h	Seawater switch malfunction; transmitter removed
RT-7	Twin cylinder; aft flexible antenna	Male	239	14 Feb. 1976	17 d	Functioning transmitter removed from dead dolphin after 21 d
RT-8	Twin cylinder; aft flexible antenna	Male	221	15 Apr. 1976	22 d	Functioning transmitter removed because of fin damage
RT-9	Twin cylinder; aft flexible antenna	Female	256	8 May 1976	10 d	Unknown. Dolphin did not bring fin above the surface
RT-10	Twin cylinder; aft flexible antenna	Female	250	9 June 1976	17 d	Unknown. Dolphin did not bring fin above the surface

[1]Inconsistent signals during the last 6 h.
[2]Direction finder malfunction after 6 d.
[3]Inconsistent signals during the last 3 d.

Visual Tags

Sixteen single bolt tags were attached between January and December 1975. One was lost within seconds, and three others were lost within 24 h. Two tags had twisted after 2 mo, damaging the fin and requiring removal of the tag. Another tag was believed to have ripped through the fin of a third animal. Two recaptured dolphins had bolt migration scars, and the tags were lost. Of 32 single bolt tags identified in the field, only 3 were sighted more than 2 wk after tagging.

From December 1975 through May 1976, 19 dolphins were tagged with double bolt tags. Tags were identified on free-ranging dolphins 187 times through July of 1976, and one tag was sighted 2 mo after attachment. Broken tags were observed eight times, and nine sightings were unidentified due to algae and barnacle fouling (Fig. 2D). Several tags were observed to have only the upper anterior edges broken, implying that breakage was from physical contact. During recaptures, four intact tags were removed because barnacles on the inner surface of the tag caused skin abrasions. Six broken tags were removed. Bolt migration was not as common as with single bolt tags, probably because of the stability offered by the rear bolt. Although none of the bolt wounds appeared fully healed, none appeared infected when the animals were recaptured and examined.

Visual tags were often discernible up to 200 m away. The numerals were rarely readable at distances >50 m, but even broken tags, tag bolts, and tag scars were useful for identification of some dolphins.

Freeze Brands

Freeze brands were recognizable on marked animals at distances of <30 m, although photographic analysis was often necessary to confirm identification. Some brands were difficult to identify because they were incomplete or because of the relatively poor color contrast of the brand against the skin (Figs. 1D, 2C).

One of the dolphins captured by Irvine and Wells (1972) in March 1971 and freeze branded (on both sides of the dorsal fin) was captured again in December 1975. The animal had a readable freeze brand on only one side of the fin. On another dolphin branded in the same manner in March 1971 and additionally recognizable because of a deformed lower jaw, the brand was readable in May 1971 (Evans et al. 1972), but the brand was no longer visible upon recapture in February 1976.

Roto Tags

From February 1976 through July 1976, 53 Roto tags were placed on 38 dolphins, including 3 animals released with 2 tags. Roto tags were known to be lost from 17 animals and were replaced on 10 of them. A healed indented notch on the trailing edge of the fin was the only evidence of tag loss. Two Roto tags were replaced due to barnacle fouling on the inner surfaces. Brown algae and/or barnacles obscured the tag numbers on most recaptured dolphins, but the tags were still readable on close examination.

Roto tag color could be observed from up to 70 m in calm seas. When examined photographically, position of the tag on the fin or placement in relation to other tags or marks helped verify identity. No dolphins were identified exclusively with Roto tags.

Spaghetti Tags

Seventeen spaghetti tags were attached to 13 dolphins, including 4 dolphins initially released with two tags. None of the animals reacted noticeably to the attachment process. Six tags were missing from four animals recaptured 10 wk after tagging. Three tags were removed from three other dolphins because the entry wounds appeared to be festering.

Animals that had lost their tags bore healed but discolored scars that were similar in size to the festering entry wounds described above. No scratches or other evidence that the dolphins may have attempted to remove the tags by rubbing were noted. The wounds, up to 1.9 cm in diameter, apparently were created by movement of the base of the tag streamer on the skin.

One spaghetti tag was observed in May 1977, 345 d after attachment. Several orange colored spaghetti tags became faded within 4 wk, an observation not reported by other investigators.

Natural Marks

Twelve untagged dolphins with recognizable natural marks were identified a total of 87 times. Photographs of an individual taken first in 1970-71, then during this study in 1976, and by Wells

et al.[6] in 1980 suggest that natural marks are relatively permanent.

DISCUSSION

The most obvious shortcoming of tags attached to the dorsal fin was the short longevity. Water drag, tissue rejection, and attempts by dolphins to shed tags may have contributed to tag loss and fin damage. We had hoped that tissue would grow tightly around the bolt sheaths and insulate the wound from bolt-induced tissue irritation; however, healing apparently never occurred while bolts were in place. Since tag wounds did not heal, different attachment methods or new designs are needed. Transmitter packages on two killer whales, *Orcinus orca*, were held for 6 mo by pins implanted diagonally to the plane of the leading edge of the fin (Erickson[7]), and may offer an alternative method of attachment. The relatively larger fin of a killer whale (vs. a dolphin) may, however, have increased chances of success. Carbon bolts attach human prosthetic devices,[8] and are another attachment method yet to be tested on marine mammals.

Radio tags have proved useful to study the ecology of small odontocetes (Evans 1971, 1974; Evans et al. 1972; Gaskin et al. 1975; Würsig 1976), but the configuration used in this study is not recommended for use on *T. truncatus*. The fin damage, premature transmitter loss, and unusual swimming behavior which we observed, may influence study results. These factors have not been previously documented. Radio tags caused no obvious behavioral effects during captive tests on *Delphinus delphis* (Martin et al. 1971). In field studies, however, the radio tagged animals have been infrequently sighted and never recaptured, so possible long-term effects of the tags on the animals are unknown.

Freeze branding proved the most durable marking method. The variability of marks on the animals captured 5 yr after branding indicates that tissue response to the branding process is inconsistent. Freeze brands have remained readable after several years in captivity, but optimal coolants, application times, and pressures have yet to be determined (Cornell et al.[9]). Our resighting, after almost 5 yr, is the longest yet reported. Twenty-one of 26 of the dolphins originally tagged in this study were observed during 1980 and had freeze brands that were either completely readable in photographs or were legible enough to confirm identifications indicated by other characteristics (Wells et al. footnote 6). Maximum longevity of freeze brands is still unknown, however.

The comparatively high incidence of spaghetti tag loss reported here is noteworthy because this tagging method has been previously used with no reports of rejection or abscess (Sergeant and Brodie 1969; Evans et al. 1972; Perrin et al. 1979). Recent tests on captive dolphins have shown, however, that tag loss may be related to tissue rejection, attachment impact, or to the angle of dart entry (Jennings[10]).

Recognition of natural marks provided useful supplementary information in our study, and has been used to study bottlenose dolphins in Texas (Gruber 1981; Shane and Schmidly[11]) and Argentina (Würsig and Würsig 1977). Close approach to the animals is usually required for field recognition, however, and we felt that photoidentification was necessary to verify most of our sightings.

This tagging study has demonstrated that repeated sightings of tagged dolphins are possible and can provide substantial amounts of information about the behavioral ecology of small cetaceans (Wells et al. 1980; Irvine et al. 1981). Selection of the tags to be used should, however, involve consideration of tagging and resighting effort, tag visibility and durability, and potential harm to the tagged animal. Visual

[6]Wells, R. S., M.D. Scott, A. B. Irvine, and P. T. Page. 1981. Observations during 1980 of bottlenose dolphins, *Tursiops truncatus*, marked during 1970-1976, on the west coast of Florida. Report to National Marine Fisheries Service, Contract No. NA80-GA-A-195, 21 p. Available Center for Coastal Marine Studies, University of California, Santa Cruz, CA 95064.

[7]Erickson, A. W. 1977. Population studies of killer whales (*Orcinus orca*) in the Pacific Northwest: a radio-marking and tracking study of killer whales. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-285615, 34 p.

[8]Anonymous. 1977. The application of high purity carbon technology for Rehabilitation Engineering Center at Rancho Los Amigos Hospital. John F. Kennedy Space Center (NASA) Report SED-77-100, 146 p. Kennedy Space Center, Cape Kennedy, FL 32899.

[9]Cornell, L. H., E. D. Asper, K. Osborn, and M. J. White. 1979. Investigations on cryogenic marking procedures for marine mammals. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-291570, 24 p.

[10]J. G. Jennings, Fishery Biologist, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. October 1978.

[11]Shane, S. H., and D. J. Schmidly. 1978. Population biology of Atlantic bottlenose dolphin, *Tursiops truncatus*, in Aransas Pass, Texas. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-283393, 130 p.

tags are most detectable, but are not durable and may damage the dorsal fin tissues. Freeze brands are durable, but not highly visible. Roto tags are of limited use for field identification except in unusual close range situations (e.g., Norris and Pryor 1970), although a combination color and location of the tag can identify an individual. For free-ranging dolphins, spaghetti tags are the only current tagging option, but identification of these tags usually requires collection of the animal. If animals are to be captured initially, combinations of tag types and use of natural marks can provide effective field identification.

Although radio tagging and tag or mark identifications are valuable tools for ecological studies of cetaceans, more development and testing of tags and attachment techniques are needed. Investigators should realize that tagging methods which are successful on one species may not work well on another species. Prior to field studies, tags should be tested on the species to be studied. We also recommend intensive follow-up sighting surveys to maximize data return and to determine the effect of tags and marks on free-ranging animals.

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LITERATURE CITED

ASPER, E. D.
1975. Techniques of live capture of smaller cetacea. J. Fish. Res. Board Can. 32:1191-1196.

EVANS, W. E.
1971. Orientation behavior of delphinids: radio telemetric studies. Ann. N.Y. Acad. Sci. 188:142-160.
1974. Radio-telemetric studies of two species of small odontocete cetaceans. *In* W. E. Schevill (editor), The whale problem: A status report, p. 385-394. Harv. Univ. Press, Camb., Mass.

EVANS, W. E., J. D. HALL, A. B. IRVINE, AND J. S. LEATHERWOOD.
1972. Methods for tagging small cetaceans. Fish. Bull., U.S. 70:61-65.

GASKIN, D. E., G. J. D. SMITH, AND A. P. WATSON.
1975. Preliminary study of movements of harbor porpoises (*Phocoena phocoena*) in the Bay of Fundy using radiotelemetry. Can. J. Zool. 53:1466-1471.

GRUBER, J. A.
1981. Ecology of the Atlantic bottlenose dolphin (*Tursiops truncatus*) in the Pass Cavallo area of Matagorda Bay, Texas. M.S. Thesis, Texas A&M Univ., College Station, 182 p.

IRVINE, A. B., M. D. SCOTT, R. S. WELLS, AND J. H. KAUFMANN.
1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. Fish. Bull. U.S. 79(4):671-688.

IRVINE, A. B., AND R. S. WELLS.
1972. Results of attempts to tag Atlantic bottlenosed dolphins (*Tursiops truncatus*). Cetology 13:1-5.

LEATHERWOOD, S., AND W. E. EVANS.
1979. Some recent uses and potentials of radio-telemetry in field studies of cetaceans. *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals, Vol. 3, p. 1-31. Plenum Press, N.Y.

MARTIN, H., W. E. EVANS, AND C. A. BOWERS.
1971. Methods for radio tracking marine mammals in the open sea. IEEE 1971 Conf. Eng. Ocean Environ., p. 44-49.

NISHIWAKI, M., M. NAKAJIMA, AND T. TOBAYAMA.
1966. Preliminary experiments for dolphin marking. Sci. Res. Whales Inst. Tokyo 20:101-107.

NORRIS, K. S., AND K. W. PRYOR.
1970. A tagging method for small cetaceans. J. Mammal. 51:609-610.

PERRIN, W. F., W. E. EVANS, AND D. B. HOLTS.
1979. Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969-76. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-737, 14 p.

SERGEANT, D. E., AND P. F. BRODIE.
1969. Tagging white whales in the Canadian arctic. J. Fish. Res. Board Can. 26:2201-2205.

WELLS, R. S., A. B. IRVINE, AND M. D. SCOTT.
1980. The social ecology of inshore odontocetes. *In* L. M. Herman (editor), Cetacean behavior, p. 263-317. Wiley Interscience, N.Y.

WÜRSIG, B.
1976. Radio tracking of dusky porpoises (*Lagenorhynchus obscurus*) in the South Atlantic: preliminary analysis. ACMRR Scientific Consultation on Marine Mammals, Bergen, Norway. 21 p.

WÜRSIG, B., AND M. WÜRSIG.
1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science (Wash., D.C.) 198:755-756.

NOTES

OFFSHORE WINTER MIGRATION OF THE ATLANTIC SILVERSIDE, *MENIDIA MENIDIA*[1]

The Atlantic silverside, *Menidia menidia*, is an abundant fish in coastal waters of the western Atlantic ranging from Florida to Nova Scotia. During spring, summer, and fall, the habitat of *M. menidia* includes intertidal creeks, marshes, and the shore zone of estuaries and embayments (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953). In such areas, ichthyofaunal surveys often cite *M. menidia* as the most numerous species encountered (Mulkana 1966; Richards and Castagna 1970; Chestmore et al. 1973; Briggs 1975; Anderson et al. 1977; Hillman et al. 1977). The entire life cycle of *M. menidia* is completed in 1 yr. Reproduction occurs in the spring, juveniles grow rapidly during the summer and reach full adult size by late fall. However, considerable uncertainty exists concerning winter ecology and habitat. In populations from Chesapeake Bay northward, Atlantic silversides are rare or absent from the shallow waters of the shore zone in midwinter (Warfel and Merriman 1944; Bayliff 1950; Hoff and Ibara 1977; Conover and Ross in press). Hildebrand and Schroeder (1928) and Richards and Castagna (1970) reported that *M. menidia* were captured in midwinter with bottom trawls in deepwater areas of Chesapeake Bay and deep estuarine channels in eastern Virginia. Catches of *M. menidia* have also been occasionally reported up to 15 km offshore (Clark et al. 1969; Fahay 1975). However, Needler (1940) noted that Atlantic silversides could be taken through the ice in Malpeque Bay, P.E.I. (although he presented no data concerning relative seasonal abundance), and investigations in South Carolina found an abundance of *M. menidia* in intertidal marsh creeks during winter (Cain and Dean 1976; Shenker and Dean 1979).

Because the Atlantic silverside is an important forage fish (Merriman 1941; Bayliff 1950; Bigelow and Schroeder 1953) and reaches a high level of biomass in the shore zone of marshes and estuaries (7.8 g/m^2 wet weight) (Conover and Ross in press), the winter movement patterns of this annual species could represent a significant pathway of energy flow from and/or within estuarine systems. This paper demonstrates that Atlantic silversides migrate offshore in winter, and we discuss aspects of their winter ecology and distribution by examining catch records of the bottom trawl survey program of the Northeast Fisheries Center (NEFC) of the National Marine Fisheries Service (NMFS).

Methods

A modern series of standardized bottom trawl surveys was begun in 1963 by the Bureau of Commercial Fisheries (BCF) Woods Hole Laboratory (Grosslein 1969). Initially, fall surveys encompassed the general range of offshore groundfish stocks of primary interest (i.e., gadoids) and thus was confined to the area between Hudson Canyon and Nova Scotia and depths from 27 to 366 m. Later, as the goals and emphasis of the survey program expanded to include a wider variety of species, both fall and spring surveys were conducted and the sampling area was extended southward to Cape Hatteras (1967). The offshore survey region was stratified into geographic zones based on depth contours and area (Grosslein 1969). A stratified random sampling design was employed to locate trawl stations within depth strata and the number of stations was allocated in proportion to stratum area. A standard No. 36 Yankee bottom trawl with a 1.25 cm stretched mesh cod end liner was towed at each station for 30 min at an average of 3.5 kn; however, spring offshore surveys since 1973 have used the larger No. 41 Yankee trawl. Stations were sampled continuously 24 h/d during cruises.

Synoptic bottom trawl surveys in the nearshore environment were begun in 1972 by the NMFS Sandy Hook Laboratory. Early surveys in the inshore region (defined as depth strata of 5-27 m) assessed the technical and geographic feasibility of using offshore sampling gear in waters as shallow as 5 m. Since autumn 1972, inshore surveys have been conducted each fall and spring with summer cruises added in 1977 and a winter cruise in 1978. Of 18 inshore cruises through 1978, most (17) included the region from

[1]Contribution No. 73 of the Massachusetts Cooperative Fishery Research Unit.

Cape Cod to Cape Hatteras, 4 included the Gulf of Maine, and 7 included the region from Cape Hatteras to Cape Fear. During 1972-75, all inshore surveys used either a ¾ modified Yankee trawl or the No. 36 Yankee trawl. Since 1976, a No. 41 Yankee trawl has been used. Towing procedures were the same as described for offshore surveys. The seasonal and geographic variation in the extent of inshore surveys reflects their evolution as a monitoring tool.

Capture data employed in this study included date, location, time, depth, surface and bottom temperatures, and number collected. Catch locations from all surveys were plotted to the nearest 10′ of latitude and longitude on depth contour maps by season. Surface and bottom temperatures and depth frequencies were plotted for each occasion that *M. menidia* were captured.

Results

Standard bottom trawl tows at 2,057 stations from inshore surveys collected 979 *M. menidia* at 107 sites (5.2% occurrence), while offshore tows at 10,209 stations captured 464 *M. menidia* at 72 sites (0.7% occurrence). Because sampling effort by season was not uniform with respect to inshore and offshore surveys or geographic zones, analysis of catch per effort data (catch frequency) was compiled by month for inshore and offshore surveys in three geographic regions (i.e., Gulf of Maine-Georges Bank, Cape Cod-Cape Hatteras, Cape Hatteras-Cape Fear). In the inshore surveys, effort was primarily concentrated in the Cape Cod-Cape Hatteras region, where the percent frequency of capture of *M. menidia* was negligible in summer, increased in November (4.9%), peaked in January (34.3%), and declined through the spring (Table 1). Number of stations sampled in the inshore surveys of the Gulf of Maine-Georges Bank and Cape Hatteras-Cape Fear regions was inadequate for monthly or regional comparisons. In offshore surveys, the monthly pattern of occurrence of *M. menidia* was similar to that of inshore surveys; catch frequency was zero in summer and autumn, peaked in January (3.8%) in the Gulf of Maine-Georges Bank and in February (11.2%) in the Cape Cod-Cape Hatteras regions, and declined thereafter (Table 2). These data support the hypothesis of an offshore winter migration.

The geographic distribution of catches by season (Fig. 1) indicates that most collections are confined to a zone within roughly 50 km of the shoreline and within the 40 m depth contour. One collection occurred 170 km from the mainland. Although most catches appear to occur between Cape Cod and Cape Hatteras and especially in the New York Bight, sampling effort among inshore surveys was much greater in this region as previously noted (Table 1). Although only four collections of *M. menidia* were observed south of Cape Hatteras (two off Cape Fear, S.C., and two off Cape Romain, S.C.; not appearing in Figure 1), no offshore or inshore surveys were conducted south of Cape Hatteras in winter when catches might be expected.

Surface temperatures recorded at 141 of the inshore and offshore stations where Atlantic silversides were captured ranged from 1° to 22°C, but 86% of these were within a range of 2°-6°C ($\bar{x}$ = 4.9°C; Fig. 2A). Bottom temperatures recorded at 135 collecting sites revealed a similar

TABLE 1.—Percent frequency of occurrence of *Menidia menidia* at stations sampled in the inshore survey region (depth strata of 5-27 m) of the NMFS bottom trawl survey program over the continental shelf of eastern North America. Catch statistics are from cruises conducted from 1972 to 1979 and are pooled by month and area of capture. The number in parentheses is the total number of stations sampled.

Month	Gulf of Maine and Georges Bank		Cape Cod-Cape Hatteras		Cape Hatteras-Cape Fear	
Jan.	—	(0)	34.3	(70)	0.0	(2)
Feb.	—	(0)	—	(0)	—	(0)
Mar.	—	(0)	21.4	(206)	0.0	(18)
Apr.	0.0	(7)	9.6	(240)	0.0	(25)
May	—	(0)	0.7	(141)	—	(0)
June	—	(0)	0.0	(33)	—	(0)
July	0.0	(3)	0.0	(41)	0.0	(47)
Aug.	0.0	(80)	0.5	(216)	0.0	(31)
Sept.	—	(0)	0.0	(150)	0.0	(82)
Oct.	—	(0)	0.2	(398)	0.0	(40)
Nov.	0.0	(10)	4.9	(183)	9.1	(22)
Dec.	—	(0)	0.0	(6)	33.3	(6)

TABLE 2.—Percent frequency of occurrence of *Menidia menidia* at stations sampled in the offshore survey region (depth strata 27-366 m) of the NMFS bottom trawl survey program over the continental shelf of eastern North America. Catch statistics are from cruises conducted from 1963 to 1979 and are pooled by month and area of capture. The number in parentheses is the total number of stations sampled.

Month	Gulf of Maine and Georges Bank		Cape Cod-Cape Hatteras		Cape Hatteras-Cape Fear	
Jan.	3.8	(159)	—	(0)	—	(0)
Feb.	0.4	(221)	11.2	(98)	—	(0)
Mar.	0.0	(386)	4.3	(925)	0.0	(18)
Apr.	0.2	(1,270)	1.5	(518)	—	(0)
May	0.0	(456)	0.0	(2)	—	(0)
June	—	(0)	—	(0)	—	(0)
July	0.0	(310)	0.0	(114)	0.0	(41)
Aug.	0.0	(522)	0.0	(336)	—	(0)
Sept.	—	(0)	0.0	(344)	0.0	(9)
Oct.	0.0	(1,265)	0.0	(1,219)	—	(0)
Nov.	0.0	(1,628)	0.0	(154)	—	(0)
Dec.	0.0	(155)	0.0	(55)	—	(0)

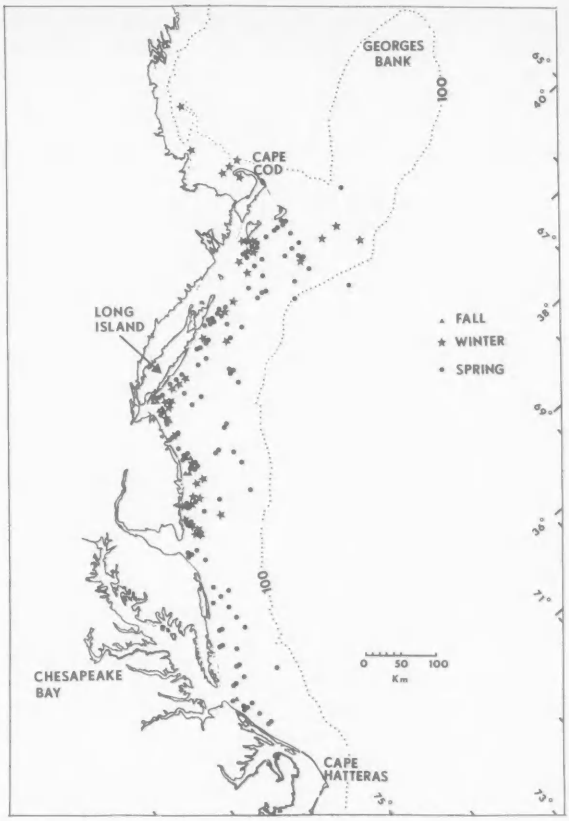

FIGURE 1.—Location of Atlantic silverside catches by season during inshore and offshore bottom trawl surveys of the National Marine Fisheries Service, Cape Hatteras to Nova Scotia, 1963-79 (fall = Sept.-Nov.; winter = Dec.-Feb.; spring = Mar.-May). Seven catch locations do not appear: Two off the northern coast of Maine, one off the outer coast of southern Nova Scotia, two off Cape Fear, S.C., and two off Cape Romain, S.C.

pattern: the majority (86%) of all Atlantic silverside collections occurred within a range of 2°-6° C ($\bar{x}$ = 5.1°C; Fig. 2B). These data indicate that *M. menidia* occur over the continental shelf primarily under winter temperature conditions after fall overturn when temperatures are isothermal.

The distribution of Atlantic silversides with respect to depth was examined by comparing catch frequency to depth of capture in 5 m intervals. The majority of catches occurred in waters <50 m deep (86%), and 42% of all catches were in depths of 10-20 m (Fig. 3). Maximum depth of capture was 126 m.

Some aspects of the winter ecology of Atlantic silversides while at sea can be revealed by examining their vertical distribution in the water column. Vertical distribution was inferred from diel variations in capture times partitioned into six 4-h intervals. Chi-square analysis comparing catch frequency in each time interval to all others combined showed that catch frequencies during night intervals (2000-0359 h) were significantly less than expected ($P<0.01$; Table 3), while catch frequencies during midday intervals (0800-1559 h) were significantly greater than expected ($P<0.01$). Apparently, *M. menidia* occurred nearer the bottom during daylight hours and hence were more susceptible to bottom trawl tows conducted during the day. These observations indicate that while at sea, Atlantic silversides are vertical migrators like other planktivores such as Atlantic herring, *Clupea harengus*, (Blaxter 1975) and American shad, *Alosa sapidissima*, (Neves and Depres 1979).

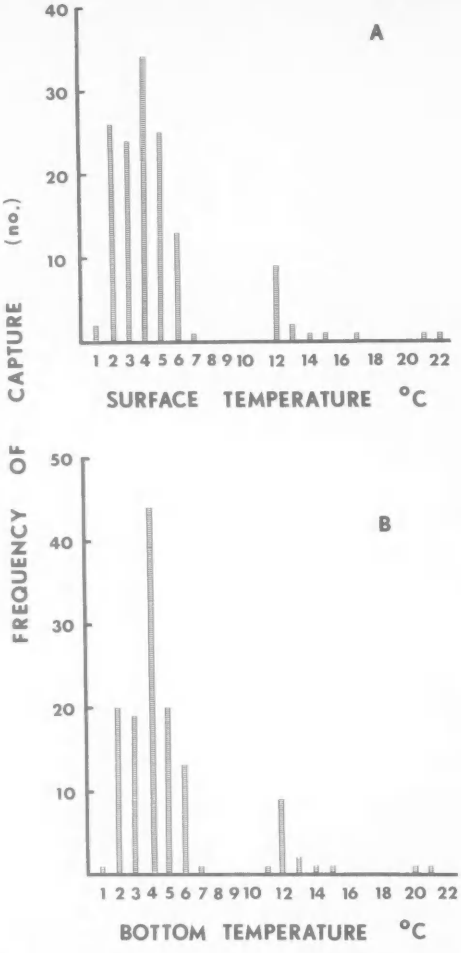

FIGURE 2.—Water temperatures at stations where Atlantic silversides were captured during inshore and offshore bottom trawl surveys conducted by the National Marine Fisheries Service during 1963-79 over the eastern North American continental shelf. A. Surface temperatures (n = 141). B. Bottom temperatures (n = 135).

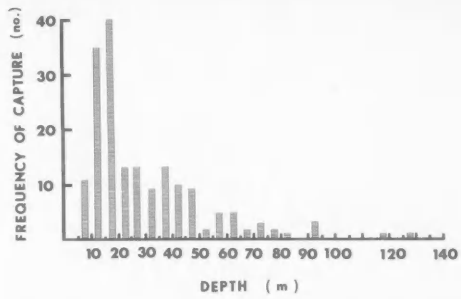

FIGURE 3.—Water depths at which Atlantic silversides were captured during inshore and offshore bottom trawl surveys of the National Marine Fisheries Service over the eastern North American continental shelf, 1963-79.

TABLE 3.—Chi-square analysis of diel variations in catch frequencies of Atlantic silversides in combined inshore (5-27 m) and offshore (27-366 m) trawl surveys conducted by NMFS, 1963-79, over the continental shelf of eastern North America.

Time of capture (e.s.t.)	Tows capturing *Menidia* (no.)		
	Observed	Expected	χ^2
0000-0359	11	29.8	14.3***
0400-0759	28	29.8	0.1
0800-1159	46	29.8	10.5***
1200-1559	43	29.8	7.0**
1600-1959	35	29.8	1.1
2000-2359	16	29.8	7.7**
Totals	179	179	

** $P<0.01$.
*** $P<0.005$.

Discussion

The results of this study demonstrate that populations of *M. menidia* north of Cape Hatteras undergo an offshore winter migration from inland to inner continental shelf waters. Atlantic silverside winter habitat probably also includes deep inland waters not sampled by NMFS surveys, as Hildebrand and Schroeder (1928) and Richards and Castagna (1970) have noted. Since the lower lethal temperature for *M. menidia* in short-term experiments was 1°-2°C (Hoff and Westman 1966; Conover unpubl. data), the offshore migration may be promoted by potentially stressful or lethal low water temperatures in shallow inland waters during midwinter. Conover and Ross (in press) and Warfel and Merriman (1944) found that Atlantic silversides leave the New England shore zone in November as water temperatures drop to about 6°-8°C. The timing of Atlantic silverside disappearance from shallow inland waters corresponds closely with their appearance in deeper offshore waters.

If the offshore migration of Atlantic silversides is primarily motivated by low temperature stress, than offshore movements in warmer waters, such as south of Cape Hatteras, would not be expected. Even though our data cannot

address this question directly, evidence from ichthyofaunal surveys in South Carolina indicate that *M. menidia* abundance remains high in intertidal creeks (Cain and Dean 1976; Shenker and Dean 1979) and in the surf zone of barrier beaches (Anderson et al. 1977) throughout winter.

The relative abundance of Atlantic silversides over the continental shelf is difficult to judge from this study, since bottom trawling is a relatively ineffective method for catching small pelagic fish such as *M. menidia* (see Conover and Ross in press). In addition, the low overall catch frequency for *M. menidia* reported herein is primarily due to the relatively small number of stations sampled in midwinter when maximum catches might be expected. Neves and Depres (1979) used similar NMFS offshore survey data on a larger pelagic species, the American shad, and reported catches at 527 of the 10,435 stations sampled (5.05%). Considering the methods used, the percent occurrences of *M. menidia* in the inshore and offshore surveys of the mid-Atlantic during midwinter (34 and 11%, respectively) may indicate considerable abundance.

In a previous study, Conover and Ross (in press) showed that Atlantic silversides reach a high level of biomass during late fall in marsh areas and also suffer a high rate of winter mortality (90-99%). Their hypothesis that winter movement and mortality patterns of *M. menidia* represent a one-way export of biomass from the shore zone of bays, marshes, and estuaries to offshore communities is strengthened by this study. The causes of high winter mortality experienced by Atlantic silversides at northern latitudes are unknown but conceivably could include predation and perhaps physiological stress imposed by the migration itself and prolonged exposure to cold temperatures. Atlantic silversides could be an important forage fish over the inner continental shelf, but it will require an analysis of the food habits of offshore fishes in midwinter to address this question.

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Literature Cited

ANDERSON, W. D., JR., J. K. DIAS, R. K. DIAS, D. M. CUPKA, AND N. A. CHAMBERLAIN.
1977. The macrofauna of the surf zone off Folly Beach, South Carolina. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-704, 23 p.

BAYLIFF, W. H., JR.
1950. The life history of the silverside *Menidia menidia* (Linnaeus). Chesapeake Biol. Lab. Publ. 90, 27 p. Solomons Island, Md.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BLAXTER, J. H. S.
1975. The role of light in the vertical migration of fish—a review. *In* G. C. Evans, R. Bainbridge, and O. Rackham (editors), Light as an ecological factor: II, p. 189-210. Blackwell Sci. Publ., Oxf.

BRIGGS, P. T.
1975. Shore-zone fishes of the vicinity of Fire Island Inlet, Great South Bay, New York. N.Y. Fish Game J. 22: 1-12.

CAIN, R. L., AND J. M. DEAN.
1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. Mar. Biol. (Berl.) 36:369-379.

CHESMORE, A. P., D. J. BROWN, AND R. D. ANDERSON.
1973. A study of the marine resources of Essex Bay. Mass. Div. Mar. Fish. Monogr. Ser. 13, 38 p.

CLARK, J., W. G. SMITH, A. W. KENDALL, JR., AND M. P. FAHAY.
1969. Studies of estuarine dependence of Atlantic coastal fishes. U.S. Bur. Sport Fish. Wildl. Tech. Pap. 28, 132 p.

CONOVER, D. O., AND M. R. ROSS.
In press. Patterns in seasonal abundance, growth and biomass of the Atlantic silverside, *Menidia menidia*, in a New England estuary. Estuaries.

FAHAY, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.

GROSSLEIN, M. D.
1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43(1), 366 p.

HILLMAN, R. E., N. W. DAVIS, AND J. WENNEMER.
1977. Abundance, diversity, and stability in shore-zone fish communities in an area of Long Island Sound affected by the thermal discharge of a nuclear power station. Estuarine Coastal Mar. Sci. 5:355-381.

HOFF, J. G., AND R. M. IBARA.
1977. Factors affecting the seasonal abundance, composition and diversity of fishes in a southeastern New England estuary. Estuarine Coastal Mar. Sci. 5:665-678.
HOFF, J. G., AND J. R. WESTMAN.
1966. The temperature tolerances of three species of marine fishes. J. Mar. Res. 24:131-140.
MERRIMAN, D.
1941. Studies on the striped bass (*Roccus saxatilis*) of the Atlantic coast. U.S. Fish Wildl. Serv., Fish. Bull. 50 (35), 77 p.
MULKANA, M. S.
1966. The growth and feeding habits of juvenile fishes in two Rhode Island estuaries. Gulf Res. Rep. 2:97-168.
NEEDLER, A. W. H.
1940. A preliminary list of the fishes of Malpeque Bay. Proc. Nova Scotia Inst. Sci. 20:33-41.
NEVES, R. J., AND L. DEPRES.
1979. The oceanic migration of American shad, *Alosa sapidissima*, along the Atlantic coast. Fish. Bull., U.S. 77:199-212.
RICHARDS, C. E., AND M. CASTAGNA.
1970. Marine fishes of Virginia's eastern shore (inlet and marsh, seaside waters). Chesapeake Sci. 11:235-248.
SHENKER, J. M., AND J. M. DEAN.
1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: Abundance, diversity and temporal variation. Estuaries 3:154-163.
WARFEL, H. E., AND D. MERRIMAN.
1944. Studies on the marine resources of southern New England. I. An analysis of the fish population of the shore zone. Bull. Bingham Oceanogr. Collect., Yale Univ. 9(2):1-91.

DAVID O. CONOVER

Massachusetts Cooperative Fishery Research Unit
Department of Forestry and Wildlife Management
University of Massachusetts, Amherst, MA 01003
Present address: *Marine Sciences Research Center*
State University of New York at Stony Brook
Stony Brook, NY 11794

STEVEN A. MURAWSKI

Northeast Fisheries Center Woods Hole Laboratory
National Marine Fisheries Service, NOAA
Woods Hole, MA 02543

GROWTH DURING METAMORPHOSIS OF ENGLISH SOLE, *PAROPHRYS VETULUS*

Among fishes, the period of transformation from the larval to adult form is marked not only by changes in morphology, behavior and in some species, habitat (Jakóbczyk 1965; Sale 1969; Hoar 1976; Marliave 1977), but in growth rate as well. Ontogenetic changes in growth have not been well documented principally because a method for determining age of larvae and juveniles has not, until recently, been available. The discovery of daily growth rings on otoliths has made possible the precise determination of age, in days, of larval and juvenile fishes (Brothers et al. 1976). Changes in growth rates during different life history stages which could be correlated with behavioral and habitat changes were observed in the French grunt, *Haemulon flavolineatum* (Brothers and MacFarland in press). Struhsaker and Uchiyama (1976) observed an inflection point in the age-length plot of larval and juvenile nehu, *Stolephorus purpureus*, indicating a change in growth rate. This inflection point corresponded with the size when body depth began to increase in proportion to the length of the fish, but not with changes in diet or habitat that occur over the course of development.

Age estimates based on counts of otolith growth increments have now allowed us to determine growth during metamorphosis of the pleuronectid *Parophrys vetulus* Girard.

Methods

The results of this study are based on the standard length (SL) in millimeters and age in days of 127 pelagic larvae and transforming individuals of *P. vetulus* ranging 10-20 mm SL, and 106 benthic 0-age individuals from 18 to 35 mm SL. Pelagic specimens were collected off Newport, Oreg. (approximately lat. 44°37'N, long. 124°06' W), from November 1977 through June 1978 with a 70 cm bongo net with 0.505 mm Nitex[1] mesh (see Laroche et al. 1982 for sampling details). Benthic *P. vetulus* were collected off Moolach Beach, Oreg., 10 km north of Newport, during September 1978 through September 1979 with a 1.5 m wide beam trawl (7 mm stretch mesh).

The removal and mounting of saccular otoliths from larvae followed the methods outlined in Methot and Kramer (1979) except that otoliths were mounted on rectangular glass cover slips to improve the optical properties of the preparation. Otolith growth increments were counted at 800 or 1250 × under bright-field illumination. A complete description of the counting technique and validation of the daily periodicity of the rings can be found in Laroche et al. (1982).

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Otoliths from the benthic individuals were removed, mounted on glass microscope slides and ground to a sagittal thin section through the nucleus using 600 grit carborundum paper. Increment counts on these ground sections were made at 250-400 × using either bright-field or polarized illumination.

The age of each fish was defined as the number of daily otolith growth increments plus five, the age at first increment formation for this species (Laroche et al. 1982).

In order to characterize changes in body form during metamorphosis, body depth, snout to anus length, lower jaw length, and the distance of migration of the left eye, of 65 larvae and 0-age benthic specimens were measured to the nearest 0.1 mm.

Results and Discussion

A plot of the length-at-age of *P. vetulus* larvae and juveniles taken in both pelagic and benthic collections exhibits a prominent plateau between 60 and 120 d of age and between 18 and 22 mm SL (Fig. 1). This plateau shows that there is a period of reduced growth in body length when these fish are undergoing metamorphosis. Plots of body depth and snout to anus length versus standard length both have a well-defined inflection point between 18 and 22 mm SL (Figs. 2, 3). Other morphometric measurement plots (lower jaw length and distance of migration of the left eye) (not shown) also contain an inflection between 18 and 22 mm SL, but less clearly. Changes in body morphology during the growth plateau are illustrated by examining a developmental series just prior to metamorphosis (Fig. 4A) and comparing individuals of similar sizes within the plateau (Fig. 4B). Changes in body depth are most pronounced, but eye migration and changes in head morphology are also evident.

The definition of two distinct growth stanzas separated by a plateau conforms to several of the criteria outlined by Ricker (1979). However, as he points out, the timing of the inflection points on the size-at-age plot depends on whether length or weight is measured. We have not measured weight in this study.

Due to the shape of the length-at-age plot we might expect the length-weight relationship for this species to be complex in form over the interval considered here.

The age of 18-20 mm SL *P. vetulus*, taken in plankton samples, was 41-74 d (about 1.4-2.4 mo) and those caught by the beam trawl, 49-116 d (about 1.6-3.9 mo; Fig. 1). The exact duration of transformation cannot be determined because of this large range. This is also illustrated by Figure 4B. The range in age of 11 pelagic specimens, 17.6-20.0 mm SL, whose left eye had begun migration, but was still on the left side of the body, was 49 d. However, if resumption of growth in body length is used to mark the end of metamor-

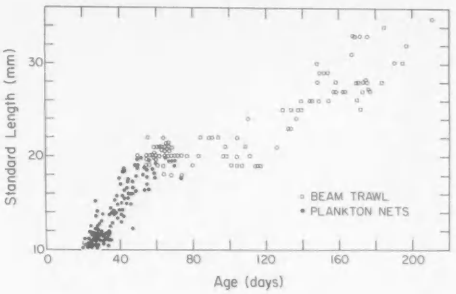

FIGURE 1.—Standard length versus age of *Parophrys vetulus* larvae and juveniles caught in plankton net and beam trawl collections.

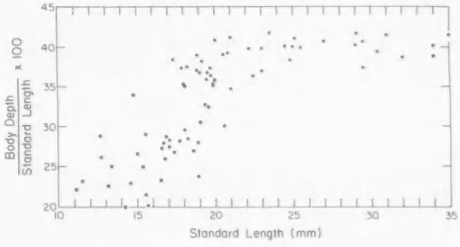

FIGURE 2.—Body depth as a percentage of standard length versus standard length of *Parophrys vetulus*.

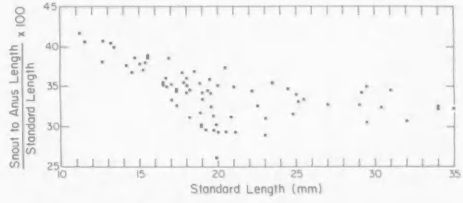

FIGURE 3.—Snout to anus length as a percentage of standard length versus standard length of *Parophrys vetulus*.

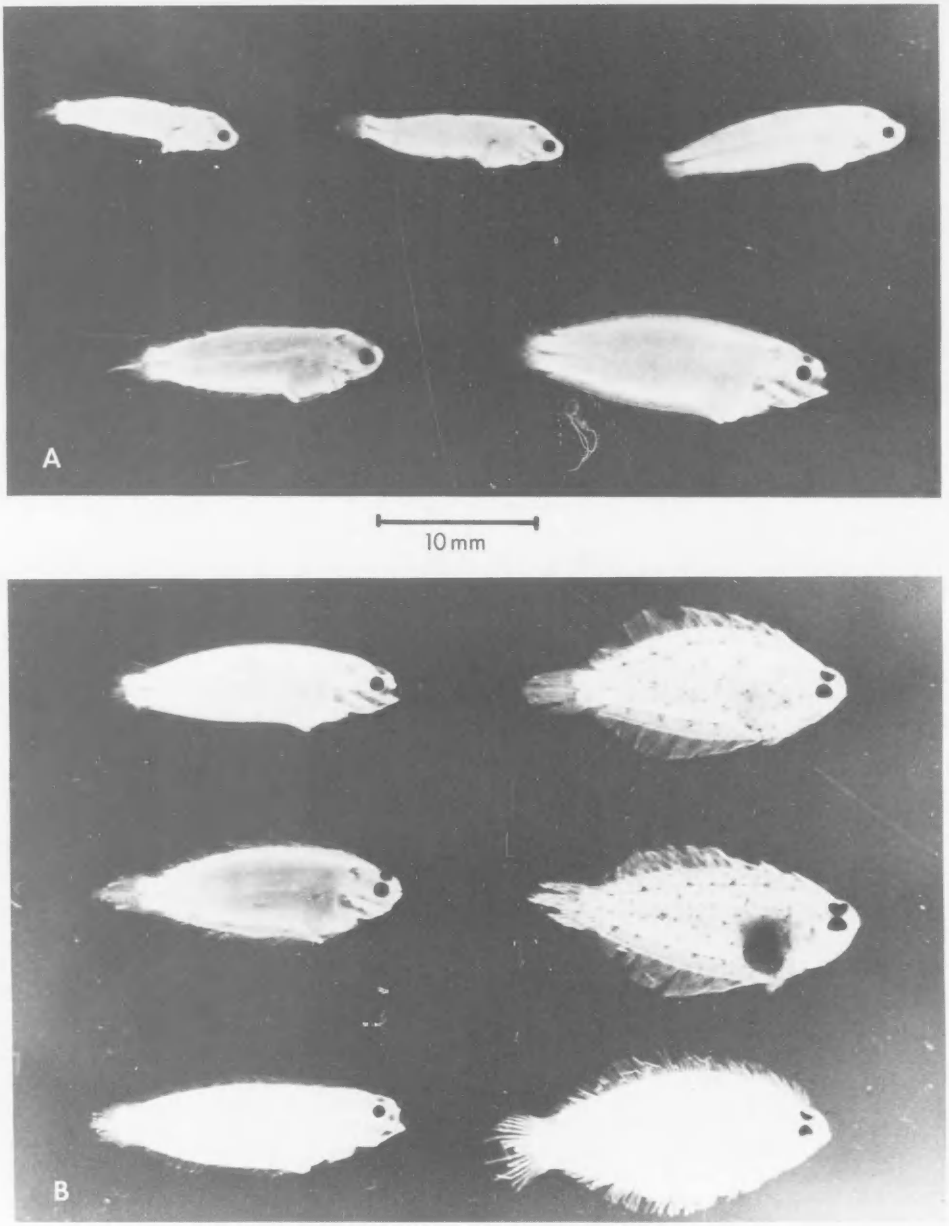

FIGURE 4.—A. Developmental series of *Parophrys vetulus* larvae. Top row, left to right, 11, 13, 14.9 mm SL; bottom 17, 19 mm SL. B. Pairs of *Parophrys vetulus* of similar lengths in different states of transformation. Top 18.0, 18.0 mm SL; middle 19.0, 19.1 mm SL; bottom 19.9, 20.0 mm SL.

phosis, then most *P. vetulus* had completed transformation by about 120 d old or 4 mo. The influence of substrate and water depth on rate of transformation in this species could be clarified only with laboratory experiments. A detailed description of body morphology versus age, as opposed to length would yield useful information on the variability in the timing of transformation. Unfortunately, we do not have such data.

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Literature Cited

BROTHERS, E. B., AND W. N. MACFARLAND.
In press. Correlations between otolith microstructure growth and life history transitions in newly recruited French grunt, *Haemulon flavolineatum*. Rapp. P.-V. Réun. Cons. Int. Explor. Mer.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

HOAR, W. S.
1976. Smolt transformation: evolution, behavior, and physiology. J. Fish. Res. Board Can. 33:1233-1252.

JAKÓBCZYK, J.
1965. Investigations on the metamorphosis of *Rhombus maximus* L. (*Pleuronectiformes*). Zool. Pol. 15:191-211.

LAROCHE, J. L., S. L. RICHARDSON, AND A. A. ROSENBERG.
1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. Fish. Bull., U.S. 80:000-000.

MARLIAVE, J. B.
1977. Substratum preferences of settling larvae of marine fishes reared in the laboratory. J. Exp. Mar. Biol. Ecol. 27:47-60.

METHOT, R. D., JR., AND D. KRAMER.
1979. The growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.

RICKER, W. E.
1979. Growth rates and models. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, Vol. VIII. p. 677-743. Acad. Press, N.Y.

SALE, P. F.
1969. A suggested mechanism for habitat selection by the juvenile manini *Acanthurus triostegus sandvicensis* Streets. Behaviour 35:27-44.

STRUHSAKER, P., AND J. H. UCHIYAMA.
1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

ANDREW A. ROSENBERG

School of Oceanography
Oregon State University, Corvallis, Oreg.
Present address: *Department of Oceanography*
Dalhousie University, Halifax, N.S. B3H 3J5 Canada

JOANNE LYCZKOWSKI LAROCHE

Gulf Coast Research Laboratory
P.O. Drawer AG, Ocean Springs, MI 39564

OBSERVATIONS ON LARGE WHITE SHARKS, *CARCHARODON CARCHARIAS*, OFF LONG ISLAND, NEW YORK

Fishermen report sightings of large white sharks, *Carcharodon carcharias*, off Long Island and southern New England every year. A popular book on shark fishing (Mundus and Wisner 1971), reported encounters with 23 large white sharks between 1958 and 1966 off Montauk Point, N.Y. Five of these were landed and weighed or estimated to range from 660 to 2,025 kg. Bigelow and Schroeder (1948) noted the occurrence of a few white sharks in southern New England waters. Otherwise most documented captures of white sharks off eastern North America are from coastal locations north of Cape Cod, Mass. (Schroeder 1938, 1939; Bigelow and Schroeder 1948, 1953, 1958; Scattergood et al. 1951; Scattergood and Coffin 1957; Scattergood and Goggins 1958; Scattergood 1959, 1962; Skud 1962; Templeman 1963; Arnold 1972). Information in these reports is limited to location sightings and morphometric observations.

We report here our detailed examinations of two white sharks landed off Long Island, N.Y., in 1964 and 1979. We also describe the feeding behavior of white sharks that were near a dead fin whale, *Balaenoptera physalus*.

Material Examined

One of us (J. G. Casey) caught a 406 cm TL (total length) immature female white shark on rod and reel 7.2 km south of Amagansett, N.Y., (lat. 40°53′ N, long. 72°06′ W) on 5 October 1964. When landed, its stomach was everted. Weight was estimated at 1,500 lb (680 kg) and morphometric measurements were taken to the nearest millimeter.

On 29 June 1979 Captain Thomas Cashman from the charter boat *Rogue* harpooned a male white shark (457 cm TL) while it fed on a 14-15 m dead and floating fin whale 24 km southwest of Moriches Inlet, N.Y., (lat. 40°32′ N, long. 72°50′ W) in 35-40 m of water. The white shark landed at Center Moriches, N.Y., weighed 2,075 lb (943 kg). The following morning we photographed, measured, and dissected the specimen. Morphometric measurements for both specimens (Table 1) follow the conventions of Bigelow and Schroeder (1948).

Biological Observations

Maturity.—The male white shark was sexually mature judging from the condition of the 40 cm claspers (Clark and von Schmidt 1965). The well-developed testes and spermatophores in the lower ductus deferens (Pratt 1979) provided additional evidence of fecund male maturity. The female was immature judging from the small size of the oviducts (approximately 1 cm in diameter).

TABLE 1.—Morphometric measurements of body parts with proportional dimensions as percent of total length.

Body part	1964 female		1979 male	
	cm[1]	% of TL	cm	% of TL
Total length	[1]406.4	100	457	100
Fork length	[2]375.9	92.5	425	93
Distance from snout to:				
eyes	27.9	6.9	27	5.9
nostrils	16.5	4.1	18	3.9
mouth	25.4	6.3	—	—
first gill (base)	99.1	24.4	100	21.9
pectoral	106.7	26.3	126	27.6
first dorsal	154.3	38.0	179	39.2
second dorsal	—	—	334	73.1
pelvic	—	—	277	60.6
anal	—	—	347.5	76.0
upper caudal pit	335.9	82.7	389	85.1
Interspace between:				
1st and 2d dorsal	99.1	24.4	110.5	24.2
2d dorsal and caudal	38.1	9.4	57	12.5
pelvic and anal	43.8	10.8	58.3	12.8
anal and caudal	30.5	7.5	43	9.4
nostrils (proximal)	19.1	4.7	20.3	4.4
Height of:				
1st dorsal	45.1	11.1	43.5	9.5
free tip	11.4	2.8	10.3	2.3
2d dorsal	7.0	1.7	6.5	1.4
free tip	8.9	2.2	7.8	1.7
Diameter of eye:				
horizontal	3.8	.9	3.5	.8
vertical	—	—	4.5	1.0
Right clasper	—	—	40.4	8.8
Left clasper	—	—	40.5	8.9
Width of mouth	43.2	10.6	37.5	8.2
Height of mouth	24.1	5.9	—	—
Max length pectoral fin	78.7	19.4	76	16.6
Girth	218	53.8	260	47.7
Weight, kg	[3]680	—	943	—

[1]Female measured in inches and converted.
[2]Calculated from total length using 92.5% (mean derived from author's unpubl. data).
[3]Estimate.

Stomach Contents and Liver.—The male's stomach and its contents weighed 52 kg when separated at the esophagus. Fifteen "bite-sized" pieces of whale blubber and muscle, 18-60 cm in diameter, in the stomach weighed 28 kg. The largest piece measured 60 × 30 × 10 cm. The stomach, distended and taut, appeared filled nearly to capacity. The liver was large, light-colored, and robust. Both lobes together weighed 178.9 kg.

Parasites.—Circumstances did not permit an exhaustive search for parasites; however, one copepod species, *Dinemoura latifolia*, was collected from the lateral surface of the caudal fin of the male.

Behavior.—One of us (R. B. Conklin) observed at least four and possibly as many as nine white sharks intermittently for 30 h (28-29 June 1979) in the vicinity of the dead fin whale. No more than two ever occurred together, and these appeared agonistic. On one occasion a 3-4 m white shark with a tooth slash over the gills approached the fin whale, then quickly changed direction and disappeared without feeding. This may have been an evasive action because seconds later a much larger male (5-6 m) appeared in the same place and began feeding on the fin whale. Some of the white sharks observed around the fin whale, including the harpooned male, had either fresh or healed tooth slashes on their sides, between the gills and caudal peduncle. These are probably not the mating cuts reported for other shark species (Stevens 1974; Pratt 1979), since they occurred on males and immature females. The tooth slashes and cuts observed on these white sharks are most likely inflicted on conspecifics while competing for prey.

Feeding behavior was observed on four occasions and probably involved different sharks. In three of the four contacts the white shark rolled and attacked with its ventral surface up (Figure 1). After the teeth were in the fin whale carcass, the white shark rolled upright thrashing its tail and cleanly cut away a mouthful of blubber. This behavior was characteristic of attacks on intact parts of the fin whale near the waterline. On the fourth occasion the white shark fed in an upright swimming position, biting on a broad piece of floating flesh.

Fishermen and film makers visited the fin whale each day from 1 to 6 July to observe and photograph the white sharks. Each morning a

FIGURE 1.—A 4 m male white shark rolling ventral side up to feed on the tail section of a dead 14-15 m fin whale. The white shark's head is under the fin whale toward the right.

white shark of 4-5 m appeared within minutes of the boat's arrival and patrolled or fed for 10-15 min. The observers believed that three to six different white sharks fed on the fin whale during this week; however, only one white shark was observed patroling and feeding at any one time after the initial discovery.

On 6 July 1979, two of us (H. L. Pratt and J. G. Casey) visited the whale carcass, which was in an advanced state of decay. A 4.5 m white shark soon appeared after the boat arrived at the fin whale. The white shark slowly circled the boat and the fin whale, then disappeared. It returned and repeated this behavior at 2-4 h intervals occasionally feeding on the fin whale.

Although the blue shark, *Prionace glauca*; shortfin mako, *Isurus oxyrinchus*; and other pelagic sharks are abundant in this area in July, they were conspicuously absent from the vicinity of the fin whale carcass. Blue sharks were being caught 5-10 km away from the fin whale. Ken Grimshaw, an experienced fish spotter pilot, made several flights over the area, and saw no blue sharks or fish schools within a 3.2 km radius of the whale. It is not unusual for fishermen to report poor catches just prior to a white shark sighting. We suggest that in these cases, the white sharks territorially exclude other species from the area.

Strength.—Based on the amount of time and size of tackle needed to land a large white shark, its strength assumes heroic proportions. The harpoon dart entered the body cavity of the 457 cm white shark forward and below the right pectoral fin, pierced the stomach and lodged in a 5 kg piece of whale blubber. The white shark then towed a 29 l keg and 26-30 m of 9.5 mm nylon line for 14½ h. Nine of these hours were spent with added resistance from the boat through 80-lb test fishing gear attached to the keg. In its final dive, it pulled a heavy nylon line out of the hands of four men. In a similar situation in June 1978, a white shark reported to be 10 m long towed Captain John Sweetman's 42-ft (12.8 m) charterboat backwards a distance of 22 km in 13 h before breaking free (Simons 1978).

Discussion

The occurrence of large white sharks in the shelf waters of the New York Bight is a well established, though often overlooked, fact. Difficulty in observing, field-identifying, and catching white sharks has resulted in a poor understanding of their presence and numbers. Their occurrence in these shelf waters may be related solely to feeding habits; however, it may also be related to reproductive activity. Judging from newspaper and other photographs, most of the large white sharks in this area are females that are approaching maturity (3-4 m FL) or are mature (4-5 m FL). At least three mature males were attracted to the dead fin whale. The presence of mature individuals of both sexes suggests that these offshore waters may be a seasonal mating ground for the white shark.

The presence of young (118-150 cm FL) white sharks in coastal waters of the New York Bight (Casey and Pratt unpubl. manuscr.) and the presence of very large females suggests that pupping may occur here or enroute during the spring migration.

Documentation in popular literature (Baldridge 1974; Ellis 1975) and commercial motion picture films indicate that white sharks attack in

an upright position. The rolling behavior reported here may be a specific pattern for feeding on large flat or slightly convex surfaces (i.e., flanks of whales).

White sharks are known to prey on seals and porpoises (Fitch 1949; Arnold 1972). Records of predation on whales are sparse and usually cited in personal communications (Randall 1973). Calculations of the energy requirements of white sharks (Carey et al. 1979), suggested that dead whales may be a primary food source for white shark populations in the western North Atlantic.

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Literature Cited

ARNOLD, P. W.
1972. Predation on harbor porpoise, *Phocoena phocoena*, by a white shark, *Carcharodon carcharias*. J. Fish. Res. Board Can. 29:1213-1214.

BALDRIDGE, H. D.
1974. Shark attack. Drake House/Hallux, Inc.

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* A. E. Parr and Y. H. Olsen (editors), Fishes of the western North Atlantic, Part one, p. 59-546. Mem. Sears. Found. Mar. Res., Yale Univ. 1.
1953. Fishes of the Gulf of Maine. U.S. Fish and Wildl. Serv., Fish. Bull. 53, 577 p.
1958. A large white shark, *Carcharodon carcharias*, taken in Massachusetts Bay. Copeia 1958:54-55.

CAREY, F. G., G. GABRIELSON, J. W. KANWISHER, O. BRAZIER, J. G. CASEY, AND H. L. PRATT, JR.
1979. The white shark, *Carcharodon carcharias*, is warm bodied. ICES (Int. Counc. Explor. Sea) C.M. 1979/H-50, 8 p.

CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci. 15:13-83.

ELLIS, R.
1975. The book of sharks. Grosset and Dunlap, N.Y., 320 p.

FITCH, J. E.
1949. The great white shark *Carcharodon carcharias* (Linneaus) in California waters during 1948. Calif. Fish Game 35:135-138.

MUNDUS, F., AND B. WISNER.
1971. Sportfishing for sharks. Macmillan Co., N.Y.

PRATT, H. L., JR.
1979. Reproduction in the blue shark, *Prionace glauca*. Fish. Bull., U.S. 77:445-470.

RANDALL, J. E.
1973. Size of the great white shark (*Carcharodon*). Science (Wash., D.C.) 181:169-170.

SCATTERGOOD, L. W.
1959. New records of Gulf of Main fishes. Main Field Nat. 15:107-109.
1962. White sharks, *Carcharodon carcharias*, in Maine, 1959-1960. Copeia 1962:446-447.

SCATTERGOOD, L. W., AND G. W. COFFIN.
1957. Records of some Gulf of Maine fishes. Copeia 1957:155-156.

SCATTERGOOD, L. W., AND P. O. GOGGINS.
1958. Unusual records of Gulf of Maine fishes. Maine Field Nat. 14:40-43.

SCATTERGOOD, L. W., P. S. TREFETHEN, AND G. W. COFFIN.
1951. Notes on Gulf of Maine fishes in 1949. Copeia 1951:297-298.

SCHROEDER, W. C.
1938. Records of *Carcharodon carcharias* (Linnaeus) and *Pseudopriacanthus altus* (Gill) from the Gulf of Maine, summer of 1937. Copeia 1938:46.
1939. Additional Gulf of Maine records of the white shark *Carcharodon carcharias* (Linnaeus) from the Gulf of Maine in 1937. Copeia 1939:48.

SIMONS, S.
1978. The real great white shark story! The Long Island Fisherman 13:18-37.

SKUD, B. E.
1962. Measurements of a white shark, *Carcharodon carcharias*, taken in Maine waters. Copeia 1962:659-661.

STEVENS, J. D.
1974. The occurrence and significance of tooth cuts on the blue shark (*Prionace glauca* L.) from British waters. J. Mar. Biol. Assoc. U.K. 54:373-378.

TEMPLEMAN, W.
1963. Distribution of sharks in the Canadian Atlantic (with special reference to Newfoundland waters). Fish. Res. Board Can., Bull. 140, 77 p.

HAROLD L. PRATT, JR.
JOHN G. CASEY

Northeast Fisheries Center Narragansett Laboratory
National Marine Fisheries Service, NOAA
Narragansett, RI 02992

ROBERT B. CONKLIN

70 Pleasure Drive
Riverhead, NY 11901

A NOTE ON THE ESTIMATION OF TRIMETHYLAMINE IN FISH MUSCLE

The chemical methods for estimation of trimethylamine (TMA) in fish muscle consist of: 1) making a protein-free extract of tissue, 2) treating with formaldehyde (FA) to fix ammonia and amines other than tertiary amines, 3) volatilizing TMA with alkali into an organic phase (toluene), and 4) measuring the degree of ionization of picric acid in toluene caused by the extracted amine.

The methods have caused controversy; they have varied in detail such that the results from different laboratories have not always been in agreement (Shewan et al. 1971).

Bullard and Collins (1980) have recently compared methods of analysis for TMA and the interference by ammonia and dimethylamine (DMA). They included the method of Murray and Gibson (1972a) and confirm that 45% KOH as alkali is optimal for the release of TMA into the organic phase. They showed that the recovery of DMA is higher than is acceptable and that DMA interferes with the assays for TMA. Murray and Gibson (1972b) had found that the interference was very low and insignificant.

Tozawa et al. (1971) showed that the concentration of FA was critical in order to minimize the interference from DMA (see their fig. 3). They found that 0.5-1.0 ml FA was optimal for a 4 ml sample and added the FA before the toluene. If less were added, significant interference from DMA occurred even with KOH as alkali rather than K_2CO_3.

Bullard and Collins (1980) added only 1 ml of 3.7% FA to the sample (4 ml) after the addition of toluene. FA and aqueous FA, which exists as methylene glycol, are soluble in toluene and thus the effective concentration of FA in the aqueous sample is probably much lower than the minimum recommended by Tozawa et al. (1971) and is in the range which would cause maximum interference by DMA.

Murray and Gibson (1972a) used 1 ml of 50% neutralized FA added before toluene. They compared their procedure with that of Tozawa et al. (1971) and found no significant differences (unpubl. results). In addition they examined chromatographically the toluene phase after extraction and found that in their procedure only TMA was extracted (Murray and Gibson 1972b).

Thus it would have been more realistic and fair to previous workers if Bullard and Collins (1980) had compared the actual published methods rather than their modifications to them and if they had specifically analyzed the material extracted into the toluene fraction. Accordingly their claim to have improved the method for TMA analysis cannot be substantiated.

It would be interesting to compare the results of analysis of samples from different species using the actual published methods done by an independent laboratory.

Literature Cited

BULLARD, F. A., AND J. COLLINS.
1980. An improved method to analyze trimethylamine in fish and the interference of ammonia and dimethylamine. Fish. Bull., U.S. 78:465-473.

MURRAY, C. K., AND D. M. GIBSON.
1972a. An investigation of the method of determining trimethylamine in fish muscle extracts by the formation of its picrate salt—Part I. J. Food Technol. 7:35-46.
1972b. An investigation of the method of determining trimethylamine in fish muscle extracts by the formation of its picrate salt—Part II. J. Food Technol. 7:47-51.

SHEWAN, J. M., D. M. GIBSON, AND C. K. MURRAY.
1971. The estimation of trimethylamine in fish muscle. *In* R. Kreuzer (editor), Fish inspection and quality control, p. 183-186. Fishing News (Books), Lond.

TOZAWA, H., K. ENOKIHARA, AND K. AMANO.
1971. Proposed modification of Dyer's method for trimethylamine determination in cod fish. *In* R. Kreuzer (editor), Fish inspection and quality control, p. 187-190. Fishing News (Books), Lond.

D. M. GIBSON

Torry Research Station
135 Abbey Road
Aberdeen AB9 8DG Scotland

SNOUT DIMORPHISM IN WHITE STURGEON, *ACIPENSER TRANSMONTANUS*, FROM THE COLUMBIA RIVER AT HANFORD, WASHINGTON

Several publications (Bajkov 1951; Semakula 1963; Vladykov and Greeley 1963; Semakula and Larkin 1968; Haynes et al. 1978; Haynes and Gray 1981) describe the behavior, natural history, and taxonomy of white sturgeon, *Acipenser transmontanus*. Although differences in snout length and shape between young and adult white sturgeon are known, morphological divergence in snout type of similar sized individuals has not been reported. We observed and documented a morphological dimorphism in the snouts of juvenile and adult white sturgeon in the Hanford reach of the Columbia River.

Materials and Methods

Sturgeon were collected in April and June 1977 with 100 m trammel nets at White Bluffs Pool (River Mile 371) on the Columbia River. Specimens were examined in the field, and total length (TL), physical characteristics, and snout types were recorded. A subsample of 10 sturgeon (41-92 cm TL), 5 designated "long snout" and 5 "short snout," was taken to the laboratory where detailed snout and head measurements were made and sex was determined (these fish were <100 cm TL to facilitate storage). All other fish were released after examination. Morphometric and meristic measurements followed Hubbs and Lagler (1958). A discriminate analysis (Morrison 1976) was used to select separating characteristics.

Results and Discussion

Field observations on 99 white sturgeon ranging from 35 to 205 cm TL showed two snout types based on size and shape. Although both snout types fit the basic characteristics of white sturgeon summarized in Scott and Crossman (1973), the short snout specimens captured at White Bluffs were more representative of that description: "...snout in adults short, depressed, bluntly rounded, shorter than postorbital length, in young sharper, longer than postorbital length; ...." The long snout was morphologically similar except for a long, slender, and pointed snout. The long snout characteristic was more pronounced in smaller immature fish measuring 35-120 cm TL, but was still evident in larger more mature individuals (Figs. 1, 2). Of the sampled population, 48% exhibited the long snout and 47% the short snout characteristics, and 5% could not be identified with either group.

Mean total length of white sturgeon examined in the laboratory was 65.50±20.63 cm for long snout and 70.62±18.79 cm for short snout fish (mean snout lengths were 6.77±1.65 cm and 6.58±0.91 cm, respectively). Of 21 morphometric and meristic measurements made on the subsample, 6 were deemed appropriate to demonstrate snout differences (Table 1). Although sample size was small, the data suggest a correlation between snout length and sex. Of the 10 sturgeon examined in the laboratory, all long snout specimens were males while 4 of 5 short snout specimens were females.

Snout type differences in white sturgeon have not been reported in other areas of the species range. The occurrence of this dimorphism at Hanford may reflect isolating mechanisms, such as physical barriers which block white sturgeon movements. Bajkov (1951) suggested that hydroelectric dams along the Columbia River isolate white sturgeon populations, preclude immigration and lead to divergent evolution. White Bluffs Pool is in the Hanford reach of the Columbia River which is bounded upstream by Priest Rapids Dam and downstream by McNary Dam. The adaptive significance of this dimorphism at Hanford is unknown.

TABLE 1.—Measurements used to demonstrate differences between five long snout and five five short snout white sturgeon.

	Long snout			Short snout		
Characteristic	Mean	SD	Range	Mean	SD	Range
Total length, cm	65.50	20.63	41.90-92.00	70.62	18.79	49.40-91.50
Head length, cm	15.13	4.03	10.30-20.95	15.59	4.00	10.70-19.35
Snout length, cm	6.77	1.65	5.05- 9.50	6.58	.91	5.50-12.50
Barbles to rostrum (B-R) ratio	4.34	.95	3.20- 5.80	3.40	.44	2.30- 3.50
Head length/snout length	2.23	.20	2.04- 2.52	2.37	.30	1.96- 2.70
Snout length/total length, %	10.34	1.71	7.62-12.18	9.32	1.46	8.98-12.20
B-R/total length, %	6.63	.87	5.50- 7.64	4.81	.95	3.50- 5.84

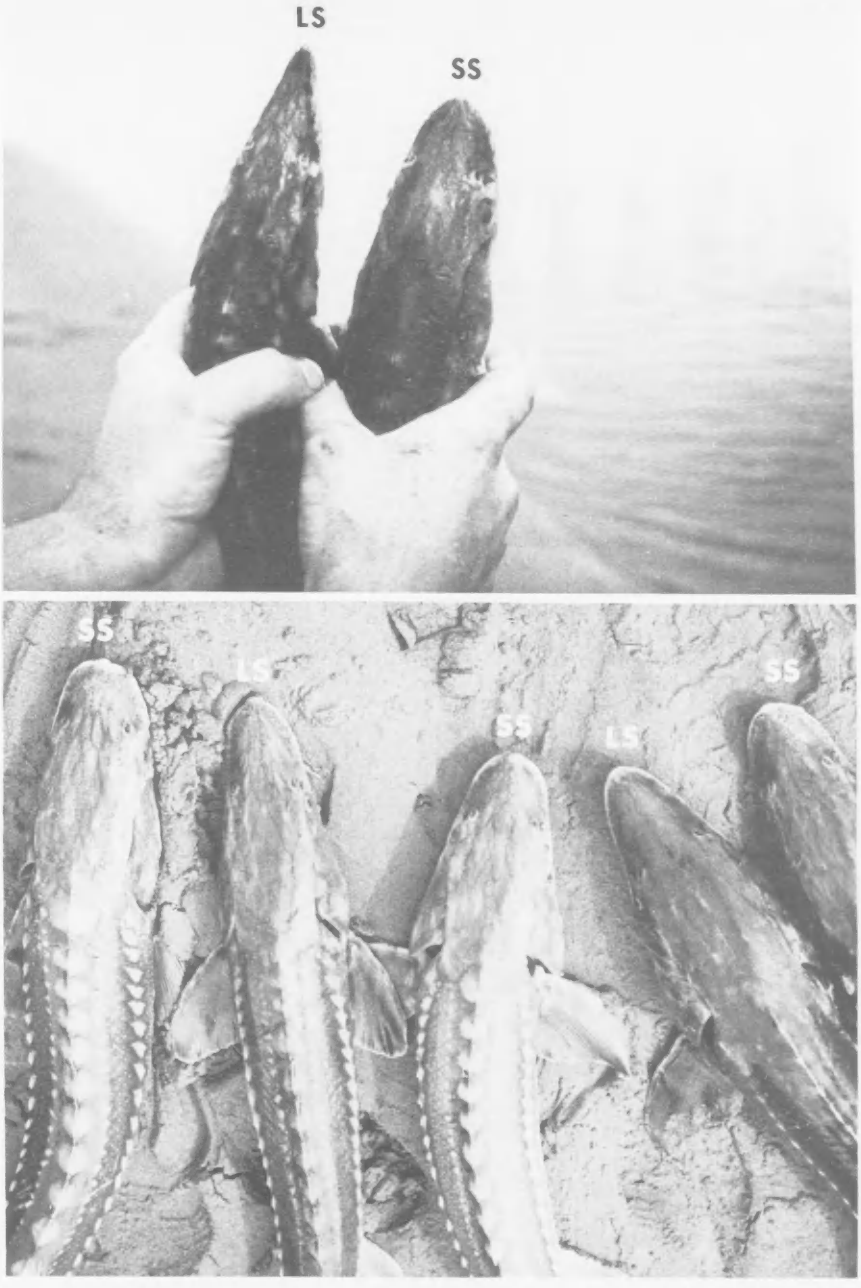

FIGURE 1.—Juvenile (above) and older (below) white sturgeon showing long (LS) and short (SS) snout characteristics.

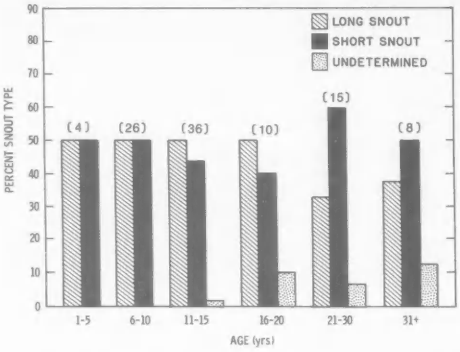

FIGURE 2.—Distribution of snout type with age for white sturgeon, *Acipenser transmontanus*, at Hanford. Age class was estimated from length based on data from Semakula (1963) for the Fraser River. Sample size in each age class in parentheses.

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Literature Cited

BAJKOV, A. D.
1951. Migration of the white sturgeon (*Acipenser transmontanus*) in the Columbia River. Oreg. Fish Comm. Res. Briefs 3(2):8-21.

HAYNES, J. M., AND R. H. GRAY.
1981. Diel and seasonal movements of white sturgeon, *Acipenser transmontanus*, in the mid-Columbia River. Fish. Bull., U.S. 79:367-370.

HAYNES, J. M., R. H. GRAY, AND J. C. MONTGOMERY.
1978. Seasonal movements of white sturgeon (*Acipenser transmontanus*) in the mid-Columbia River. Trans. Am. Fish. Soc. 107:275-280.

HUBBS, C. L., AND K. F. LAGLER.
1958. Fishes of the Great Lakes region. Revised ed. Cranbrook Inst. Sci. Bull. 26., 213 p.

MORRISON, D. F.
1976. Multivariate statistical methods. 2d ed. McGraw-Hill, N.Y., 415 p.

SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish. Res. Board Can., Bull. 184, 966 p.

SEMAKULA, S. N.
1963. The age and growth of the white sturgeon (*Acipenser transmontanus* Richardson) of the Fraser River, British Columbia, Canada. M.S. Thesis, Univ. British Columbia, Vancouver, 115 p.

SEMAKULA, S. N., AND P. A. LARKIN.
1968. Age, growth, food, and yield of the white sturgeon (*Acipenser transmontanus*) of the Fraser River, British Columbia. J. Fish. Res. Board Can. 25:2589-2602.

VLADYKOV, V. D., AND J. R. GREELEY.
1963. *Order* Acipenseroidei. *In* Y. H. Olsen (editor), Fishes of the western North Atlantic, Part three, p. 24-60. Mem. Sears Found. Mar. Res., Yale Univ. 1.

DENNIS W. CRASS

Freshwater Sciences, Ecological Sciences Department
Battelle Pacific Northwest Laboratory
Richland, WA 99352

ROBERT H. GRAY

Environment, Health and Safety Research Program
Battelle Pacific Northwest Laboratory
Richland, WA 99352

Address all correspondence to Gray.

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